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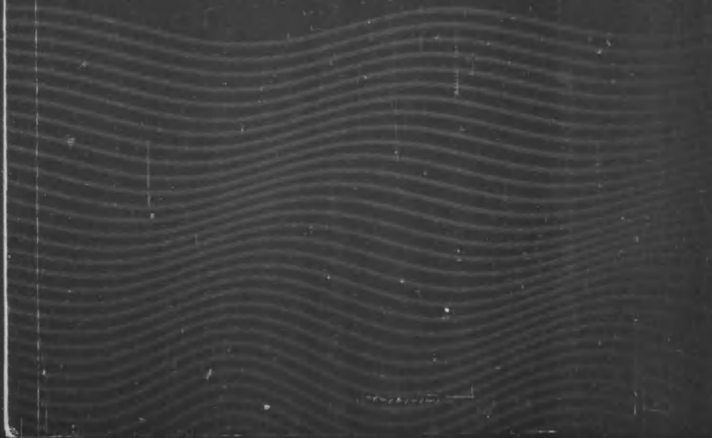

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Towards Dynamic Biological Oceanography and Limnology[1]

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Legendre, L., and S. Demers. 1984. Towards dynamic biological oceanography and limnology. Can. J. Fish. Aquat. Sci. 41: 2–19.

A new approach that couples the study of biological and hydrodynamic processes has progressively emerged in the biological oceanographic and limnological literature. A review of a large number of papers on phytoplankton, zooplankton, and fish larvae published in the last decade brings out the major characteristics of a new discipline, termed by the authors "dynamic biological oceanography" or "dynamic biological limnology." These studies recognize hydrodynamics as the driving force of aquatic ecosystems, so that the various physical, chemical, and biological factors of the environment are considered as the proximal agents through which hydrodynamic variability is transmitted to living organisms. A central idea to dynamic biological oceanography and limnology is that different hydrodynamic processes and different biological responses occur on different spatial and temporal scales. This leads to a discussion of spatial and temporal scales on both the horizontal and vertical axes and of the relationships between the physical and biological scales, on the one hand, and the sampling scale, on the other. Anticipated forthcoming developments concern the eventual merging of horizontal and vertical studies in an integrated approach to aquatic ecosystems and the design of new sampling techniques and schemes to probe the significant scales of variation in dynamic biological oceanography and limnology. Common lines of research are suggested for the coming years.

Une nouvelle tendance est apparue progressivement dans les travaux d'océanographie et de limnologie biologiques, qui combine l'étude des processus biologiques avec celle des processus hydrodynamiques. Une revue de nombreuses recherches, publiées au cours de la dernière décennie sur le phytoplancton, le zooplancton et les larves de poissons, a permis de dégager les principales caractéristiques d'une nouvelle discipline, appelée par les auteurs «océanographie biologique dynamique» ou «limnologie biologique dynamique». On constate dans ces travaux que ce sont les forces hydrodynamiques qui entraînent les écosystèmes aquatiques, alors que les divers facteurs physiques, chimiques et biologiques du milieu sont les agents immédiats qui assurent la transmission de la variabilité hydrodynamique vers les organismes vivants. L'idée que différents processus hydrodynamiques et différentes réponses biologiques se produisent aux différentes échelles spatiales et temporelles constitue un pivot de l'océanographie et de la limnologie biologiques dynamiques. Ceci conduit à considérer les échelles spatiales et temporelles en fonction des axes horizontaux et verticaux ainsi que les relations qui existent entre, d'une part, les échelles physiques et biologiques et, d'autre part, l'échelle d'observation. Les prochains développements envisagés ont trait à une éventuelle unification, dans un concept intégré d'écosystème aquatique, des études menées sur l'horizontale et la verticale ainsi qu'à la mise au point de nouvelles techniques et de nouveaux plans d'échantillonnage, permettant d'explorer les échelles de variation significatives en océanographie et en limnologie biologiques dynamiques. On propose aussi des orientations communes de recherche pour les années à venir.

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In the last decade, new types of studies have progressively appeared in both the oceanographic and limnological literature, in which the biological processes are coupled with the physical hydrodynamic processes. These studies concern mainly the pelagic environment, i.e. phytoplankton, zooplankton, and fish larvae, but such benthic organisms as molluscs, for instance, are now being considered along the same lines, as they are directly linked to the pelagic environment through filter feeding. As phytoplankton respond directly to variations in the physical environment, it is not surprising that dynamic biological oceanography and limnology first focussed on this trophic level, which explains the large number of studies published to date. Such an approach is not as obvious for the higher trophic levels, where the proximal determinants of biological responses include other living organisms, resulting in a smaller number of published papers. These studies, which were at first conducted more or less independently by a few laboratories and are now part of a growing trend, are progressively leading towards a new approach in biological oceanography and limnology. By analogy with dynamic physical oceanography, we suggest calling this new approach "dynamic biological oceanography" or "dynamic biological limnology." As any other discipline, dynamic biological oceanography or limnology will eventually refer to a set of fundamental principles, sampling and/or experimental strategies, and data reduction procedures. It is, of course, too early to define such bases for dynamic biological oceanography and limnology, but some examples of these terms of reference will be outlined in the remainder of our paper.

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[1] J. C. Stevenson Memorial Lecture (1984), delivered by L. Legendre.

Development of Dynamic Biological Oceanography and Limnology

Early Studies

The first researchers to explicitly link biological dynamics to hydrodynamics were probably Gran and Braarud (1935), who invoked the lack of vertical stability of the water column to explain the small phytoplankton numbers observed in the Bay of Fundy. A few years later, Bigelow et al. (1940) suggested that differences in vertical stability could account for differences in the time of the spring bloom in the Gulf of Maine. These previous studies and the analysis of his own data led Riley (1942) to conclude "that the balance between the effects of vertical turbulence and the increasing vernal radiation determines the beginning of the spring diatom flowering." Using Riley's farsighted concept, Sverdrup (1953) defined the "critical depth," i.e. the depth to which the mixed layer must be confined before the spring bloom can occur. It must be recognized at this stage that the proximal agent of the spring bloom is light, since critical depth determines the mean light conditions in the mixed layer. The critical depth model won rapid recognition and is now the classical explanation of the spring bloom found in textbooks of biological oceanography or limnology.

As to the relationship between the dynamics of zooplankton and hydrodynamics, Riley and Bumpus (1946) suggested that vertical mixing of the water column, combined with vertical migrations, could explain differences between distributions of zooplankton and those of phytoplankton. Unfortunately, these ideas remained untested by lack of suitable data.

Renewed interest in the hydrodynamic control of biological processes started at the beginning of the 1970s under the influence of several factors. Among them was the high biological variability evidenced at meso and small scales by studies in shelf and lake waters, which had been conducted at much smaller temporal and geographical scales than the classical oceanographic surveys. Small-scale sampling would have been impossible without the development of new techniques such as the continuous measurement of chlorophyll *a* by in vivo fluorescence (Lorenzen 1966). Simultaneously, the introduction in aquatic ecology of such numerical techniques as spectral analysis (Platt 1972) made it possible to analyze the series of continuous measurements, thus leading to the development of new models (see, e.g., Denman and Platt 1976; Denman et al. 1977). Another significant factor was the growing number of physiological studies on the responses of phytoplankton to light variations, which turned out to be fundamental in explaining the control of phytoplankton production by hydrodynamics.

Phytoplankton: Horizontal Structure

It has been known for many years that phytoplankton is not distributed uniformly at the surface of oceans and lakes. After reviewing the data available three decades ago, Bainbridge (1957) did conclude that phytoplankton patches vary in a continuous series, from a few metres across to as much as 50–75 × 220–300 km, their mean size being about 20 × 75 km. To explain this patchiness, he invoked wind-induced water movements and restricted upwelling of nutrient-rich water. An alternative explanation was provided by the "KISS" model of Kierstead, Slobodkin, and Skellam (Kierstead and Slobodkin 1953; Skellam 1951), where both horizontal diffusion and phytoplankton growth rate are used as input parameters. Given these two parameters, the model calculates a critical patch size, below which diffusion disperses any horizontal structure built up by phytoplankton growth.

Many studies of the last decade were devoted to describing the patchy distribution of phytoplankton. The size of phytoplankton patches was estimated from in vivo fluorescence records, and from series of cell counts and of assimilation numbers (P^B: production per unit chlorophyll), resulting from intensive sampling programs. In estuarine, coastal, and oceanic waters, the characteristic magnitude of phytoplankton patches is ~1 km (Table 1). However, such patches were not always found (Table 1, footnotes c and d; Horwood 1978; Sinclair et al. 1980). It must be noted that patch size is not the same for different seasons and areas (Table 1, footnote b; Fasham and Pugh 1976) and that in vivo fluorescence spectra, from which patch size is often estimated, can vary considerably in time (Demers et al. 1979; Wilson et al. 1979). In lakes (Table 1), the size of phytoplankton patches varies with the size of the basin, from tens of metres to a few kilometres. Patches can have an elongated form, stretched in the direction of prevailing winds (Abbott et al. 1979) or currents (Levasseur et al. 1983).

The new approaches to the description of phytoplankton patches naturally led to investigations into the mechanisms that control patchiness. Most of the studies used spectral analysis to partition the variance of phytoplankton series according to frequencies (time^{-1}) or wave numbers (length^{-1}) and to compute coherency spectra between phytoplankton and environmental variables. The overall results are as follows.

1) At horizontal scales smaller than 1 km (Platt 1972) or even 5–10 km (Denman and Platt 1975; Steele 1975, 1976), phytoplankton distribution is dominated by horizontal turbulent diffusion. In highly energetic environments, the scale may be pushed up to many tens of kilometres (Sinclair et al. 1980).

2) At some critical scale (typically ~1 km, see Table 1) and up to 5 km, phytoplankton growth overcomes horizontal turbulent diffusion, which results in increased spatial heterogeneity (Denman and Platt 1975; Denman 1976; Lekan and Wilson 1978). At this scale, Therriault and Platt (1978) also found that the spatial distribution of phytoplankton is, on some occasions, affected by zooplankton grazing. In addition, patches of this size are very sensitive to wind velocities: in conditions of low turbulent mixing (wind $\leq 5\ \text{m}\cdot\text{s}^{-1}$), phytoplankton patchiness is induced by local differences in growth rates, while in conditions of high wind ($\geq 5\ \text{m}\cdot\text{s}^{-1}$), spatial variations are damped out by horizontal turbulent processes (Therriault et al. 1978; Therriault and Platt 1981). In an estuarine environment subjected to strong tidal currents, stronger winds would be needed to homogenize the horizontal distribution of phytoplankton (Levasseur et al. 1983).

3) At larger scales, i.e. typically over 5 km, phytoplankton patchiness is controlled by mesoscale (1–100 km) water motions (advection, eddies, local upwelling, etc.) (Fasham and Pugh 1976; Estrada and Wagensberg 1977; Lekan and Wilson 1978; Gower et al. 1980). These scales are those that have been reviewed by Bainbridge (1957) (see above), and it is remarkable that the physical mechanisms then invoked are very close to

TABLE 1. Characteristic scales of phytoplankton patches.

Sampling area and season	Scale (km)	Source
Bedford Basin, summer	0.8–1.9	Platt and Filion 1973[a]
Long Island Sound, August	1–5	Lekan and Wilson 1978
North Atlantic (temperate), spring[b]	~1	Fasham and Pugh 1976
North Atlantic (tropical), August[b]	~1	Fasham and Pugh 1976
North Sea, spring	None[c]	Horwood 1978
St. Lawrence Estuary, June	0.1–1	Denman 1976
St. Lawrence Estuary, June	≤5	Denman and Platt 1975
St. Lawrence Estuary, August	~0.75	Fortier et al. 1978
St. Lawrence Estuary, July	0.2–6	Levasseur et al. 1983
St. Lawrence Estuary, August	None[d]	Sinclair et al. 1980
St. Margarets Bay, autumn	~1–3	Platt et al. 1970
St. Margarets Bay, summer	0.5–1.6	Platt et al. 1970[a]
Lake Tahoe, September	~0.1	Powell et al. 1975
Lake Tahoe, September	>0.1–<10	Richerson et al. 1978
Castle Lake	0.06	Richerson et al. 1978

[a] Actual calculations of patch size in Platt et al. (1977).

[b] Critical patch size smaller in stable tropical conditions than in temperate spring bloom.

[c] From a few metres up to 21 km, no critical wavelength was found above which biological processes dominate over turbulent ones.

[d] Physical control of phytoplankton distribution up to ~100 km.

those evidenced in recent and more sophisticated studies. The upper limit of this control by mesoscale physical processes is still undefined, since most phytoplankton series are relatively short. Tentative minimum values are 21 km (Horwood 1978), 40 km (Fasham and Pugh 1976), and 50 km (Estrada and Wagensberg 1977), while satellite imagery suggests an order of 100 km (Gower et al. 1980). In Long Island Sound where nutrients changed with the transition from estuarine to coastal waters, Lekan and Wilson (1978) found a relation between the structure of chlorophyll and that of nutrients at a scale larger than 20 km.

The above results also apply to lakes, with some changes in scales. In Lake Tahoe, Powell et al. (1975) showed that phytoplankton growth supersedes horizontal turbulent diffusion, in dominating phytoplankton distribution, at a scale of about 100 m. In addition, Leigh-Abbott et al. (1978) demonstrated that different spatial patterns of chlorophyll can be found in two different regions (midlake and nearshore) of Lake Tahoe: at large scales (100–1000 m), the two regions differed primarily because of differences in nutrient import, while at intermediate scales (10–100 m) it was because of differences in the mixing regime. In a small productive lake, George and Heaney (1978) found that wind velocities $>1.2\ \mathrm{m \cdot s^{-1}}$ were sufficient to break down patches of phytoplankton, which is a much lower velocity than that ($5\ \mathrm{m \cdot s^{-1}}$) reported by Therriault et al. (1978), Therriault and Platt (1981), and Levasseur et al. (1983) for marine coastal environments (see above).

A major conclusion of these studies is that the causes of patchiness are different on different scales, which explains why spectral analysis played a major role in the statistical analysis of phytoplankton series. Indeed, spectral analysis partitions the variance of the data series, or the covariance between two series, among the observed spatial (wave numbers) or temporal (frequencies) scales. As a consequence, new models had to be developed to interpret the spectral characteristics of the phytoplankton series.

As discussed above, the KISS model of the early 1950s explained that the growth of phytoplankton maintains the integrity of patches against horizontal diffusion for aggregations larger than a characteristic length scale. Platt and Denman (1975) and Wroblewski et al. (1975) have modified the KISS model to include the effect of zooplankton grazing. Since herbivore grazing reduces the net growth rate of the phytoplankton, the critical size for patch formation is then larger than given by the KISS model. Wroblewski et al. (1975) also concluded that it was necessary to include nutrient limitation in the KISS model to achieve realistic patch dynamics for the oceanic regime. Another way to refine the KISS model is to incorporate the fact that the diffusion of phytoplankton cells is scale dependent (Okubo 1978).

In view of interpreting actual phytoplankton spectra, Denman and Platt (1976) used the basic ideas of the KISS model and combined them with the theory of turbulence to produce by dimensional analysis an equation for a theoretical phytoplankton spectrum (Fig. 1a). An alternative equation was derived by Denman et al. (1977), using an approach developed for the study of reacting mixtures in a turbulent fluid (Fig. 1b). Contrary to that of Denman and Platt (1976), this second model did not assume that there is a range of wave numbers within which the convective effect can be ignored compared with the effect of phytoplankton growth. Both theoretical treatments predicted that the slope of the spectrum should change in the vicinity of the characteristic length scale k_c (analogous to the critical patch size of the KISS model: see above). However, the first model predicts a bend (a "knee") in the spectrum, while the second predicts a peak, which defines a preferred wave number region for phytoplankton variance.

Spectra have been computed for phytoplankton series, but also for series of physical (temperature, currents, Richardson number) or chemical (nutrients) variables, with the intention of determining the scales over which phytoplankton is related, or not, to environmental variables. For instance, differences between slopes of temperature and chlorophyll spectra at low wave numbers (large scale) were often attributed to phyto-

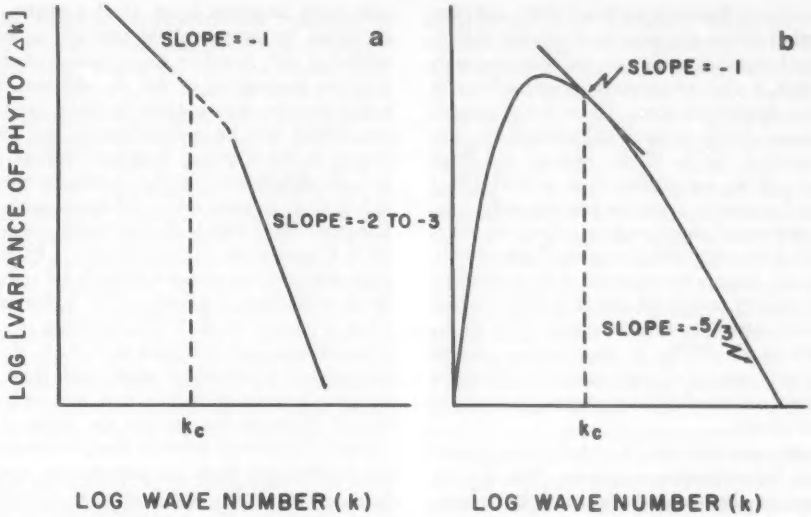


FIG. 1. Schematic theoretical spectra (a, Platt and Denman 1976; b, Denman et al. 1977) for the horizontal variability of phytoplankton. The predictions of the two models, as to the regions demarcated by the characteristic wave number k_c, are as follows:

$k \gg k_c$	Turbulent motions dominate the horizontal distribution of phytoplankton. Slope between -2 and -3	Phytoplankton spectrum follows the velocity spectrum, with a slope of $-5/3$
$k \approx k_c$	Phytoplankton growth and turbulent energy dissipation are of comparable importance	Effect of convective mixing just balances that of phytoplankton growth
$k \ll k_c$	Phytoplankton growth dominates the horizontal distribution. Slope of -1	There is a preferred wave number region for phytoplankton variance at $k \approx 0.25\ k_c$

plankton growth. Using a stochastic modification of the KISS model, Fasham (1978a) demonstrated that phytoplankton spectra observed in nonequilibrium growth conditions (e.g. blooms) are likely to show a similar slope to temperature spectra. Thus, a similar slope on phytoplankton and temperature spectra cannot be used to infer a physical control of phytoplankton. As a final caution, Star and Cullen (1981) demonstrated that nonmonotonic relationships between phytoplankton and environmental variables do obscure the results of spectral analysis.

Despite the fact that in the above models, maintenance and development of patches is explained by phytoplankton growth, the literature contains few studies on the patchiness of growth rates. Platt and Filion (1973) observed significant variability in the assimilation number at the scale of a few kilometres. Similar results were also reported by Therriault and Platt (1978) and ascribed to either taxonomic or physiological patchiness (Therriault and Platt 1981).

Zooplankton grazing obviously plays some role in phytoplankton patchiness, which explains why it was incorporated into the KISS model (see above) by Platt and Denman (1975) and Wroblewski et al. (1975). Dubois (1975a, 1975b) combined Lotka–Volterra prey (phytoplankton)–predator (zooplankton) relationships with diffusion to compute a critical patch size for phytoplankton. Riley (1976) proposed a model that explains mesoscale phytoplankton patchiness by the interaction of zooplankton vertical migrations with tides and residual drift. Finally, models of Steele (1974) and Levin and Segel (1976) suggest that the interaction between diffusion, predators, and prey can lead to persistent patchiness, the generation of patches not being entirely unidirectional (breaking up of larger structures into smaller), since small patches can contribute to patterns at larger scales.

The very existence of phytoplankton patches, each with different properties (Platt and Filion 1973; Therriault and Platt 1981), is consistent with the "contemporaneous disequilibrium" hypothesis of Richerson et al. (1970) that extended the work of Margalef (1967). According to this hypothesis that explains the "paradox of the plankton" (Hutchinson 1961), the pelagic environment resembles a mosaic of microhabitats in which the different species have differential growth characteristics. These spatial inhomogeneities contribute in ensuring the stability of marine ecosystems (Dickie 1973; Steele 1974; Platt and Denman 1975).

Phytoplankton: Vertical Structure

Most of the attempts to describe and interpret the horizontal structure of phytoplankton were conducted without considering the vertical distributions of properties in the water column. On physical grounds, Kullenberg (1978) suggested that vertical processes, in combination with the vertical shear of horizontal processes, could play an important role in generating horizontal patchiness on scales up to about 10 km. Using the Richardson number as an index of potential stability of the water column, Fortier and Legendre (1979) concluded that variations in vertical stability could control the mesoscale phytoplankton dynamics. In the same vein, Denman and Platt (1975) and Denman (1976) interpreted differences observed between chlorophyll and temperature horizontal series recorded simultaneously at two different depths as the consequence of internal waves propagating on strong density gradients. The action of internal waves on the horizontal distributions of chlorophyll was also invoked by Kamykowski (1974, 1976), Fasham and Pugh (1976), Haury et al. (1979), and Cullen et al. (1983). Other mechanisms such as Langmuir circulation can also induce the concentration or dispersion of phytoplankton cells in the water column (Ryther 1955; Pincemin 1969; Evans and Taylor 1980). Vertical mixing can also modify the response of phytoplankton populations to such primary sources of spatial heterogeneity as variable nutrient concentrations or differential grazing by zooplankton (Powell et al. 1975). In these cases, vertical processes are additional sources of mechanical variation that add up to the horizontal turbulent diffusion already included in the KISS model (see above).

According to the time scale considered, vertical processes are not met by the same phytoplankton responses. This is what Harris (1980a) showed in a hierarchical scheme of phytoplankton responses to the spectrum of environmental fluctuations. According to this scheme, when perturbations are small or rapid, only physiological responses are observed; however, if the stimulus is of greater amplitude or longer lasting, the responses then go higher and higher in the hierarchy until ultimately growth rates and taxonomic changes do occur. The major time scales of vertical processes to which phytoplankton are known to respond are annual, seasonal, neap-spring tidal (M_f: 13.7 d), a few days, semidiurnal (M_2: 12.4 h), and Langmuir circulation (30 min). Phytoplankton responses to each time scale will be reviewed briefly, as will be their underlying mechanisms.

On an annual scale, changes in vertical stability of the water column account for the spring bloom and the following period of phytoplankton growth (see above and Gilmartin 1964). They also account for changes in the taxonomic composition of phytoplankton populations (Wangersky 1977; Bowman et al. 1981) and in the vertical distribution of phytoplankton communities (Venrick 1972; Ignatiades 1979; Haffner et al. 1980). In lakes, the photosynthetic parameters are strongly related to the annual variations in thermal stability of the water column (Harris et al. 1980).

On a seasonal scale (two summer months), Demers and Legendre (1982) demonstrated that changes in the stratification characteristics of an estuarine water column are reflected in both the photosynthetic capacity ($P^B_{\max}$) and the variance of chlorophyll. Increasing density stratification has two effects on the phytoplankton: a physiological effect in the form of a light-dependent increase in the photosynthetic capacity and a population response in the form of an increase in chlorophyll variability.

A number of phytoplankton characteristics were found to be associated with the neap-spring (M_f) tidal variations of vertical stability in estuarine and coastal areas: chlorophyll concentrations (Sinclair 1978; Takahashi et al. 1977, as reinterpreted by Webb and D'Elia 1980), cellular chlorophyll content (Demers et al. 1979), amplitude of the circadian variations of photosynthetic capacity (Demers and Legendre 1981), and primary production (Winter et al. 1975, as reinterpreted by Sinclair 1978). During spring tides there is intense vertical mixing and decreased vertical stratification that results in the deep vertical mixing of phytoplankton cells and an eventual increased loss of cells from the photic layer. Deeper mixing in the spring tides decreases the average light intensity to which the cells are subjected and therefore their photosynthetic activity, which explains neap-spring cycles. In addition, in areas where the mixed layer becomes nutrient depleted, spring-tidal destratification favors nutrient replenishment, and thus, phytoplankton growth in the following neap-tidal period. In summer fronts, periodic enrichment of surface waters by nutrients, followed by stabilization at neap tides, delineates areas of the Northwest European Shelf with high chlorophyll concentrations (Pingree 1978; Pingree et al. 1975, 1976, 1977, 1978), while patterns of phytoplankton succession vary with the vertical mixing characteristics (Holligan and Harbour 1977). Similarly, on the Scotian Shelf (Fournier et al. 1979), changes in winter chlorophyll concentrations are correlated with 15- to 60-d variations in the steepness of a subsurface shelf-break front. Enhanced phytoplankton production in this case was attributed to decreased frontal steepness that reduces the depth of the mixed layer. Similar relationships between frontal structures and phytoplankton distributions were also reported by Iverson et al. (1979), Seliger et al. (1981), and Perry et al. (1983). According to the local conditions, the proximal agents of neap-spring phytoplankton cycles are therefore either light (depth of mixing) or nutrients (replenishment/depletion) or a combination of both.

On the time scale (a few days) associated with the passage of frontal disturbances (Heath 1973; Walsh et al. 1977), physical transient phenomena (winds, storms, periodic upwelling, etc.) are other destabilizing agents of the water column that influence phytoplankton. In coastal marine waters, Iverson et al. (1974), Takahashi et al. (1977), and Legendre et al. (1982a) reported intermittent summer phytoplankton blooms that followed stabilization of a water column previously destabilized by wind. Côté and Platt (1983) also showed, in a small marine inlet, that the normal progression of phytoplankton community structure was periodically perturbed by transient phenomena. This time scale is very critical, since Kemp and Mitsch (1979) have shown that there is a relationship between species diversity and vertical mixing. In their model, coexistence of three phytoplankton species in the same ecological niche was possible only if a random turbulent component was added to the hydrodynamic function, with a frequency approaching 1 cycle$\cdot$d^{-1} that is the turnover rate of the phytoplankton.

On the semidiurnal (M_2) tidal scale, two different conditions of vertical mixing can be encountered by phytoplankton cells. In areas and at times of moderate mixing, the cells are vertically mixed to depths that vary semidiurnally, being thus subjected to an average light intensity that varies on a semidiurnal or a quarterdiurnal (M_4: 6.2 h) cycle. In contrast, under conditions of intense and persistent vertical mixing, phytoplankton cells are subjected to an average light cycle that is no longer circatidal but becomes circadian. Phytoplankton responses will therefore differ according to the intensity and persistence of vertical mixing, since the light history of the cells is known to influence the photosynthesis–irradiance relationship (Steemann-Nielsen and Hansen 1959; Ryther and Menzel 1959; Beardall and Morris 1976; Marra 1978a; Falkowski 1980). In addition, light and shade adaptation can modify the photosynthetic pigments (Steemann-Nielsen 1975; Beardall and Morris 1976; Prézelin 1976), the proportion of light-harvesting pigments relative to P_{700} (reaction-center chlorophyll) (Thornber et al. 1977), the photosynthesis–irradiance curves (Steemann-Nielsen and Jorgensen 1968), and the photosynthetic unit (PSU) (Prézelin 1981; Perry et al. 1981).

In conditions of moderate vertical mixing, changes in environmental conditions are slower than physiological adaptation by the phytoplankton, so that the cells can continuously adjust their metabolic activities to the new conditions (Vincent 1980). In the Lower St. Lawrence Estuary, there are reports of 12- to 13-h cycles in chlorophyll (Therriault and Lacroix 1976; Fortier and Legendre 1979) and in photosynthetic capacity (Fortier and Legendre 1979; Fréchette and Legendre 1982). A 6-h endogenous periodicity in chlorophyll synthesis was also observed in the same estuary by Auclair et al. (1982). The latter is in agreement with a physiological model of light and shade adaptation, based on changes in the rates of chlorophyll synthesis (Falkowski 1980). Recently, Falkowski (1983) reported variations in the chlorophyll/P_{700} ratio (an index of the size of the photosynthetic units or PSU) that were related to vertical mixing. Since the chlorophyll/P_{700} ratio responds rapidly to vertical mixing, it was suggested that this indicator of the recent light history of the cells may provide information about vertical mixing processes.

In contrast, when vertical mixing is intense and persistent, changes in environmental conditions become more rapid than the adjustment time of the phytoplankton, so that the cells can acclimate only to the mean environmental conditions (Savidge 1979; Falkowski 1980). In a well-mixed area of the middle St. Lawrence Estuary, Demers and Legendre (1979, 1981) observed only circadian periodicities in the photosynthetic capacity ($P^B_{\max}$) of the phytoplankton, despite tidally controlled variations in chlorophyll concentrations.

Langmuir vortices are generated in surface waters at wind speeds in excess of a critical value ($\sim 4\ \mathrm{m \cdot s^{-1}}$) (Harris and Lott 1973b). At the time scale (~30 min) corresponding to Langmuir vertical circulation, Harris and Lott (1973a), Jewson and Wood (1975), Harris and Piccinin (1977), Harris (1978), and Marra (1978a, 1978b) demonstrated, both in the laboratory and for natural waters, a positive response of marine and freshwater phytoplankton photosynthesis to the cyclically changing light intensity. This is due to shortened residence time of phytoplankton cells in the surface layer, with the result that high rates of photosynthesis can be maintained before photoinhibition and photorespiration become prevalent (Harris 1980b). However, the effect of this mechanism on the integrated water column primary productivity is debatable (Falkowski and Wirick 1981).

Another effect of local meteorological variations is small-scale turbulence, which was demonstrated by Savidge (1981) to affect growth kinetics, nutrient uptake, and photosynthesis of marine phytoplankton cultures. He concluded that this is not an effect of diffusion limitation, but rather that agitation controls the rates of various specific physicochemical processes (adsorption, active uptake, etc.).

After considering the wide range of vertical processes that affect phytoplankton, Legendre (1981) concluded that only the alternation of stabilization and destabilization is an hydrodynamic mechanism conducive to enhancement of primary production. It follows that the phytoplankton production potential of marine ecosystems increases with their frequency of stabilization and destabilization, since the resulting input of mechanical energy does enhance the primary production.

High-frequency (0.1–10 Hz) light fluctuations caused by water surface waves are another type of vertical light fluctuations in the water column. They were reported to either increase or decrease phytoplankton production (Dera et al. 1975; Fréchette and Legendre 1978). These seemingly contradictory results were explained by Walsh and Legendre (1982) who demonstrated in the laboratory that the photosynthetic response varies according to the frequency (0.1–10 Hz) of the fluctuating light regime. Further work at sea (Walsh and Legendre 1983) showed that phytoplankton photosynthesis is affected by the color of the fluctuating light, the response of the population being also influenced by its taxonomic composition. Since the frequency of these light fluctuations changes with depth (Gordon et al. 1971), Walsh and Legendre (1982, 1983) suggested that the photosynthetic maximum in the water column may well be a response to the vertical distribution of not only light intensities but also light fluctuation frequencies. In addition, light fluctuations of lower frequency caused by cloud cover were found to be correlated with variations in phytoplankton fluorescence (4×10^{-3} to 3.5×10^{-2} Hz) (Abbott et al. 1982) and in carbon uptake (2.7×10^{-4} to 2.2×10^{-3} Hz) (Gallegos et al. 1980). It follows that short-term light variations probably play an important role in structuring the vertical distribution of phytoplankton properties.

The above considerations on both the horizontal and vertical structures of phytoplankton do stress the fact that in hydrodynamically active areas, phytoplankton production is controlled by neither light nor nutrients. The control of phytoplankton production is exerted by hydrodynamics through the proximal agency of light and/or nutrients. Furthermore, a distinction must be made between state variables, such as temperature or chlorophyll, and rate variables, such as mixing rate or photosynthetic assimilation. The former variables vary in the long term or on large scales, while the latter react rapidly and on small scales. In dynamic biological oceanography and limnology, physical and biological variables are tightly related, so that biological dynamics can be used to estimate hydrodynamics. Such as approach was suggested for both state and rate variables; e.g. Gower et al. (1980) did use surface chlorophyll patchiness as an indicator of the fluctuation spectrum of mesoscale oceanic structures, and Falkowski (1983) estimated the vertical mixing rate of phytoplankton from the vertical variations in chlorophyll/P_{700} ratios.

Zooplankton

Studies on the horizontal distribution of zooplankton arose from the fact that the spatiotemporal heterogeneity of these organisms is a major cause of error in estimating their local biomass (Cassie 1963). Zooplankton patches have been observed on a wide range of spatial and temporal scales. Reported patch size varies from a few centimetres (micropatches) to several thousand kilometres (megapatches) (Haury et al. 1978). The explanatory mechanisms of zooplankton heterogeneous distribution are still somewhat uncertain (Lee and McAlice 1979), but they generally refer to some physical factors (transition zones, advection, turbulence) or biological properties (reproductive rate, social or specific behavior, intraspecific interactions) or a combination of both physical and biological factors. According to Longhurst (1981), the aggregation of zooplankton is a necessary condition of life in the aquatic environment and it is probably the most fundamental reason why the mechanisms controlling zooplankton heterogeneity are studied.

The factors that control the horizontal distribution of zooplankton become easier to identify as patch size increases. On the scale of ocean basins, heterogeneities have been identified for the biomass and the species composition of zooplankton (Beklemishev 1969; McGowan 1971, 1974; Bachus et al.

1977). These biogeographic structures are generally associated with the main features of the oceanic circulation (McGowan 1974). Similarly, patches on the scale of 100–1000 km are related to such large-scale systems as the Gulf Stream (Wiebe et al. 1976b; Wiebe and Boyd 1978; Boyd et al. 1978), the California Current (Brinton 1967; McGowan 1967), or the circulation in the Gulf of Mexico (Maul et al. 1974). Studies on large scales demonstrate the influence of both physical and biological factors on the abundance of zooplankton (Fager 1963).

The mesoscale (1–100 km) distribution of zooplankton has been the subject of several studies. Structures on these scales are often associated with upwelling areas, in which case the location of the biomass maximum is determined by the intensity of the upwelling (Andrews and Hutchings 1980; Smith et al. 1981). The zooplankton concentrations often develop in band(s) parallel to the coast that can eventually be transported offshore (Andrews and Hutchings 1980). Even if zooplankton maxima usually overlap chlorophyll maxima (Peterson et al. 1979; Andrews and Hutchings 1980; Walsh et al. 1980), they do not seem to be the result of in situ grazing and growth but rather are the consequences of physical transport and behavioral aggregation within the upwelling zone (Peterson et al. 1979; Andrews and Hutchings 1980). George and Edwards (1976) reached the same conclusions about the effect of wind-driven upwelling on the distribution of plankton in a shallow lake. According to Peterson (1979), the interaction between vertical migrations and upwelling circulation reduces the transport of organisms outside the upwelling area, thus favoring the maintenance of mesoscale heterogeneities.

On the scale of 1 m to 1 km, structures in zooplankton biomass or species composition are mainly related to such local hydrodynamic features as coastal fronts, internal waves, or tides (Cassie 1963; Wiebe 1970; Fasham et al. 1974; Smith et al. 1976). This scale of variation was much studied, due to the large error it introduced in the estimation of zooplankton biomass (Wiebe and Holland 1968; Wiebe 1971, 1972; Wiebe et al. 1973; Chanut 1975). This error increases with increased heterogeneity of the physical environment (Haury 1976b). For example, in such highly dynamic environments as estuaries, variations in zooplankton biomass are mainly related to tidal advection processes (Lee and McAlice 1979; Gagnon and Lacroix 1981, 1982, 1983; Maranda and Lacroix 1983).

Small-scale simultaneous studies of zooplankton and physical structures were made possible by the development of new equipment capable of simultaneously sampling physical variables and zooplankton. These are the Longhurst–Hardy plankton recorder (Longhurst and Williams 1976), the undulating oceanographic recorder (Bruce and Aiken 1975), and the "batfish" vehicle (Dessureault 1976) equipped (Herman and Dauphinee 1980) with an in situ electronic zooplankton counter (Boyd 1973); other techniques such as high-frequency echo-sounding (McNaught 1968) and multiple opening and closing nets (Wiebe et al. 1976a; Sameoto et al. 1980) were also used to investigate zooplankton small-scale structures. The first studies using this equipment showed zooplankton patches from 13 to 300 m (Wiebe 1970; Fasham et al. 1974), and they concluded that there was hydrodynamic control of zooplankton heterogeneity at this scale. However, the lack of appropriate physical measurements prevented firm conclusions as to the underlying mechanisms.

Small-scale heterogeneities can be associated with internal waves or frontal structures (Pingree et al. 1974; Haury 1976a; Haury et al. 1979, 1983; Herman et al. 1981; Zeldis and Jillett 1982). In such areas, the size and orientation of patches may result (Zeldis and Jillett 1982) from the interaction between the vertical circulation caused by internal waves and the behavior of organisms, which try to maintain themselves in a given water stratum. In other studies, zooplankton aggregation was explained solely by the mechanical effect of the internal wave or of the front in concentrating the organisms (Haury et al. 1979; Herman et al. 1981). Strong relationships between chlorophyll and zooplankton biomass were similarly ascribed to internal waves by Mackas et al. (1980), Star and Mullin (1981), and Haury et al. (1983). In all cases, however, the data cannot unambiguously establish if the responses of zooplankton to environmental (physical or biological) variations were passive or active. When zooplankton aggregates seem to be a response to phytoplankton biomass (Mackas et al. 1980; Star and Mullin 1981; Herman et al. 1981), it must be remembered that the ultimate control of zooplankton patchiness is then exerted by hydrodynamics, since the high chlorophyll concentrations are themselves caused by internal waves or a front. In this case, phytoplankton become the vector through which hydrodynamically induced heterogeneity is transferred to higher trophic levels.

In areas subjected to active hydrodynamics, both environmental and behavioral factors are probably involved in the generation and persistence of small-scale zooplankton patches. In oceanic waters, however, where the fine-scale physical environment is more homogeneous, zooplankton patchiness is caused mainly by biological interactions (grazing, predation, social and reproductive behavior) and zooplankton mobility (Haury and Wiebe 1982). As a result, the relative intensity of zooplankton patchiness in these environments is greater than that of the phytoplankton (Fasham 1978b; Mackas and Boyd 1979).

The distribution of zooplankton is also vertically heterogeneous. Acoustic methods (high-frequency echo-sounding) have been used to follow changes in the vertical and horizontal distributions of zooplankton (Pieper 1979; Sameoto 1983). These studies were mainly descriptive and also very speculative as to the factors that controlled the observed heterogeneities. The significance of vertical distribution of zooplankton was also stressed by Evans (1978), who modeled the horizontal plankton patchiness in terms of the vertical distributions of nutrients, phytoplankton, and herbivores that are induced by vertical shear. Other works have shown that maximum zooplankton biomass is generally at the depth of the chlorophyll maximum (Anderson et al. 1972; Mullin and Brooks 1972; Hobson and Lorenzen 1972; Youngbluth 1975; Gunderson et al. 1976; Haury 1976a; Fairbanks et al. 1980; Ortner et al. 1980) or at the depth of maximum phytoplankton production (Venrick et al. 1973; Longhurst 1976a; Herman et al. 1981). Since the vertical distance between the chlorophyll and production maxima is often relatively small (~10 m), Herman et al. (1981) explained the disagreement above by a sampling and/or sampler resolution too coarse to resolve such a fine difference, so that the argument remains open. This coupling between the vertical distribution of zooplankton and that of phytoplankton may be of great importance in areas with high grazing activity, since many models of phytoplankton patchiness include the grazing rate as an input parameter (see above).

A common conclusion from most studies on zooplankton distribution is that it was not possible to unambiguously identify the physical and/or biological factors that controlled the generation and maintenance of aggregates. This is due to the fact that, most often, resulting effects were investigated rather than causal mechanisms. This problem could be resolved if zooplankton rate (physiological) properties were measured in addition to state (biomass) characteristics (Cox et al. 1982). As an example of such an approach, Cox et al. (1982) used enzyme activities of laminariase in zooplankton samples as an index of grazing activity (time lag of ~2 d). In the California coastal upwelling, they found that equilibrium between zooplankton grazing rates and phytoplankton production is a function of both zooplankton localization behavior and the upwelling-driven circulation. A complex interplay between these two factors determines whether or not equilibrium is ever approached. According to Cox et al. (1982), the spatial coherence between phytoplankton and zooplankton is an indicator of the level of complexity of the prevailing physical dynamics in the upwelling area.

Other studies have demonstrated the possibility of measuring such physiological rates as grazing or respiration, using enzyme activities that are changing proportionally to the rate of the physiological process (Boucher and Samain 1974; King and Packard 1975; Boucher et al. 1976; Mayzaud and Conover 1976; Mayzaud and Poulet 1978; Mayzaud 1980, 1981; Mayzaud and Mayzaud 1981; Cox 1981; Cox and Willason 1981; Hassett and Landry 1982). For the grazing rate, there is a suggested change of enzyme concentration in response to the density of food, so that enzyme activities could be used to estimate in situ the grazing responses to differential phytoplankton concentrations (Cox et al. 1982). The development of such methods, combined with intensive sampling programs on both environmental and zooplankton rate variables, should lead to significant advances in dynamic biological oceanography and limnology.

Fish Larvae

Fisheries biologists have developed two radically different approaches to the long-term prediction of commercial stocks. On the one hand, stock–recruitment models (Ricker 1954) are based on the assumption that the number of recruits is regulated by the density of spawners. On the other hand, the early-survival approach, which can be traced back to Hjort (1914), hypothesizes that recruitment depends on the success or failure of the annual colonization of the environment by the larvae, their survival being independent of the initial number of eggs produced.

Within the framework of this second approach, there are several hypotheses to explain the observed annual variations in recruitment, and thus in early survival. Most of these hypotheses postulate that availability of suitable food is the main determinant of survival. For instance, the larval drift hypothesis states that spawning strategies have been developed so that drifting larval fish can reach nursery areas with high primary and secondary production where survival is maximized (Pearcy 1962). The same idea is known as the match/mismatch hypothesis (Cushing 1972), which postulates a dependence of larvae survival on the timing between spawning and the cycle of primary and secondary production. Alternatively, the stability hypothesis (Lasker 1975) ascribes early survival to the persistence of local food aggregates, which can sometimes be dispersed by such environmental perturbations as storms or abnormal circulation.

In these theories pertaining to the early-survival approach, food is recognized as the proximal determinant of larval survival, while hydrodynamics are the forcing mechanism that drives the system. As suggested by Fortier (1982), this is analogous to phytoplankton (see above), where growth is forced by or phased on hydrodynamics, through the proximal agency of light and/or nutrients. In the last decade, a number of large-scale correlative studies have linked fish larvae and microzooplankton (Jones 1973; Ware 1977; Wyatt 1980; Frank and Leggett 1982; Sameoto 1982) as well as year-class strength and hydrodynamics (Sutcliffe 1973; Stevens 1977; Nelson et al. 1977; Bailey 1981). However, only a few recent investigations have postulated that survival of fish larvae is primarily controlled by hydrodynamics and have designed integrated physical and biological surveys to test such hypotheses. These studies follow the same general trend as described above for phytoplankton and zooplankton, thus linking fisheries ecology with dynamic biological oceanography and limnology.

Three recent publications can be used to illustrate this new approach. These studies were all conducted in the partially mixed middle St. Lawrence Estuary, where circulation is two-layered. They were based on simultaneous time series of larval and microzooplankton (third study) samples and of physical oceanographic measurements (temperature, salinity, and currents). Fortier and Leggett (1982) first demonstrated that the transport of newly hatched larvae is purely passive. Selection of appropriate spawning grounds, combined with precise emergence levels relative to the residual circulation, ensures the geographical separation of the two dominant species: newly hatched Atlantic herring (*Clupea harengus harengus*) larvae are passively transported landward in the deeper layer, while capelin (*Mallotus villosus*) larvae emerge in the seaward flowing surface layer. The second publication (Fortier and Leggett 1983) showed that later larval stages of Atlantic herring performed semidiurnal vertical migrations that were synchronized with the M_2 tides, so that these larvae experienced limited seaward drift. By contrast, migrations of capelin were nycthemeral and of small amplitude, so that this species remained close to the surface. As a result, Atlantic herring larvae are retained in the upper reaches of the middle estuary where zooplankton biomass is high, and capelin larvae are transported towards an area of the lower estuary where primary productivity is maximum in the summertime. In their third publication, Fortier and Leggett (1984) established that the horizontal distribution of Atlantic herring larvae is significantly correlated with the distribution of microzooplankton at the time of yolk sac resorption, which stresses the importance of food aggregates for the survival of early larval stages. These results were achieved by using small-scale, high-frequency sampling, which shows again that the interaction between hydrodynamics and biological processes can be studied only on a spatiotemporal scale that is compatible with the phenomenon at hand.

The idea of hydrodynamic control of larval survival that had emerged from large-scale correlative studies (see above: Sutcliffe 1973; Stevens 1977; Nelson et al. 1977; Bailey 1981) was further developed by Iles and Sinclair (1982). Their hypothesis is that year-class variability is largely independent of reproduction, growth, or other population parameters and is instead determined by the confinement of larvae in "larval retention areas." These are zones where hydrodynamics (tidal mixing) and larval behavior interact so as to maintain an aggregated population of Atlantic herring larvae for several months. The larval retention areas identified by Iles and Sinclair (1982) lie to a large degree within vertically well-mixed zones bounded by temperature fronts. According to this hypothesis, year-class variability becomes a function of the variability in the "retention" characteristics of the larval environment.

There is therefore a current trend in fisheries ecology, as in phytoplankton and zooplankton studies, to recognize hydrodynamics as the driving force of aquatic ecosystems. In such a perspective, the various physical, chemical, and biological factors of the environment act as proximal agents through which hydrodynamic variability is transmitted to living organisms. The above studies on phytoplankton, zooplankton, and fish larvae have shown that aquatic organisms "have evolved mechanisms not only to cope with such variability but to actively exploit it" (Harris 1980a).

Major Characteristics of Dynamic Biological Oceanography and Limnology

Physical and Biological Scales

The investigations on phytoplankton, zooplankton, and fish larvae, reviewed in the previous section, share several common trends. Their hypotheses, sampling designs, data analyses, and ecological interpretations are all founded upon a tight coupling between hydrodynamics and biological dynamics. In contrast with the more traditional approaches where average relationships are sought, this physical–biological coupling is structured in space and time so that the physical scales on which the phenomena occur become central to the research. It is also recognized that different hydrodynamic processes and different biological responses occur on different scales. This fact determines (or should determine) the choice of the physical and biological variables to be investigated. For practical reasons, most of the works have been limited to only two physical dimensions until recently. For instance, studies on spatial horizontal scales are generally conducted without considering the vertical and temporal dimensions, studies on the temporal variability of vertical profiles (yo-yo anchor station) do not often explicitly refer to the horizontal dimensions, and studies on changes in the vertical structures along a transect (batfish) normally have no lateral resolution or temporal component.

A central idea to dynamic biological oceanography and limnology is that different hydrodynamic processes and different biological responses occur on different spatial and temporal scales. The four components of any study (physical and biological variables, temporal and spatial scales) are not independent in the aquatic environment so that the choice of any one as the focus of the investigation narrowly limits the choice of the remaining three. This constraint is of practical advantage, since it determines, for instance, what are the proper spatial and temporal scales and what is the most appropriate physical variable to be considered in studying a given biological response, or what are the physical and biological variables most indicative of ongoing processes to be studied on given spatial and temporal scales, and so on. Of course, much more work is needed before unequivocal relationships are established between spatial and temporal scales and physical and biological variables for the various compartments of the aquatic ecosystem (phytoplankton, zooplankton, fish larvae, etc.). Such a correspondence for the phytoplankton is tentatively derived from Harris (1980a, fig. 1) and shown in Table 2. Similar scaling schemes could eventually be worked out for the zooplankton and the fish larvae.

TABLE 2. Correspondence between spatial and temporal scales for hydrodynamics and phytoplankton. All the possible processes that occur at these scales are not accounted for. Derived in part from Harris (1980a, fig. 1).

Spatial scale	Temporal scale	Hydrodynamics	Biological dynamics
Mesoscale	Seasonal	Advection, eddies	Community structure
Kilometres	Days	Turbulent diffusion	Biomass, growth rates
Small scale	Short term	Turbulent mixing	Physiology

Even if some aspects of Table 2 may be somewhat debatable, it can be used to stress and explain the major trends of dynamic biological oceanography and limnology. Every physical and biological property in the aquatic environment varies within only a narrow range of scales (Table 2). If a property that varies on a given scale is sampled on a much larger scale, two classes of problems may arise. The first is that the large-scale structures then observed may not be interpreted correctly. On a large scale, for example, heterogeneities in biomass may not be attributed to changes in communities, as they should if biomass had been sampled rather than community structure. The second class of problems consists of artificial large-scale structures that can be numerically generated when the sampling scale is larger than the scale on which the observed property varies. This phenomenon is known as "aliasing" in time series analysis. As an example, let us consider an organism with a life cycle of 15 d. If it is sampled fortnightly, the 15-d cycle will be obliterated; on the other hand, if the sampling interval is 20 d, an artificial 60-d cycle will be generated (Fig. 2). On the contrary, if a property is sampled on a much smaller scale than that on which it varies, then possibly no variations will be detected. This might lead to the conclusion, for instance, that there is no hydrodynamic control of phytoplankton on the sampled scales or that there is no predator–prey relationship, while variables more relevant to these scales might have shown the opposite. As an example, temperature spectra typically have a $-5/3$ slope over a wide range of scales, and chlorophyll spectra are often as in Fig. 1. The variance spectrum of temperature is representative of the spatial heterogeneity of a passive environmental "contaminant," while the smaller slope of the chlorophyll spectrum at low wave numbers (large structures) was often attributed to phytoplankton growth (see above). However, Fortier and Legendre (1979) caution against such an interpretation, since the spectrum of an active hydrodynamic property (Richardson number: an index of potential vertical stability) may itself be different from that of temperature at intermediate frequencies (Fig. 3). This suggests that vertical stability might be a more relevant variable than temperature on these scales, especially in assessing the hydrodynamic control of phytoplankton.

From the works reviewed above, it is apparent that the approach to the horizontal heterogeneity is generally quite different from that of the vertical structure. This can be explained by reference to the scaling scheme worked out in Table 2 for the phytoplankton and the eventual corresponding schemes for zooplankton and fish larvae. An obvious difference between the vertical and the horizontal axes is their respective spatial extension, which is much smaller on the vertical than on the horizontal. Actively growing phytoplankton are generally confined to the mixed layer, i.e. vertically to a few tens of metres. On the continental shelf, zooplankton and fish larvae

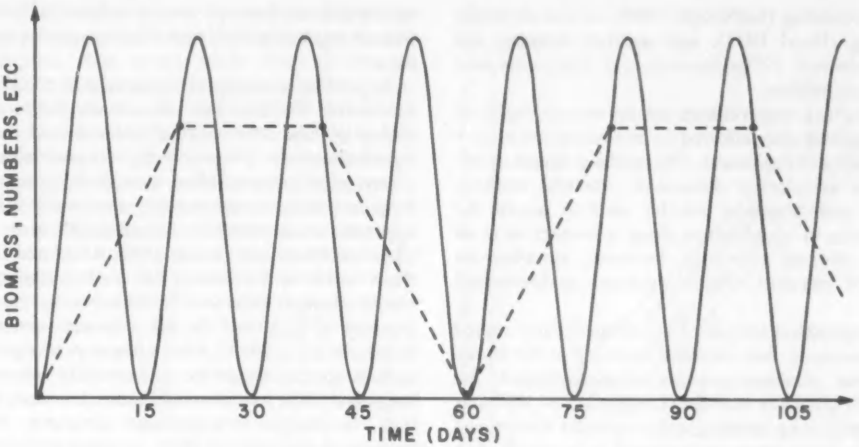


FIG. 2. Artificial 60-d cycle (broken line) as the result of sampling a 15-d cycle every 20th d.

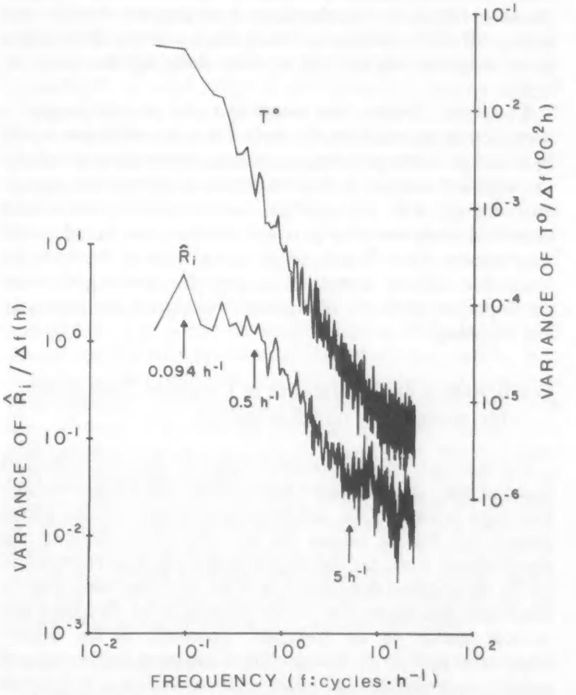


FIG. 3. Smoothed spectra for the Richardson number ($\hat{R}_i$) and temperature (°C) in the St. Lawrence Estuary (adapted from Fortier and Legendre 1979).

can migrate a few hundred metres at maximum between the surface and the bottom. However, actual vertical movements of zooplankton are often much more limited, and in the open ocean, diel vertical migrations do not normally exceed hundreds of metres (Longhurst 1976b). In contrast, horizontal structures can extend up to at least 100 km (Gower et al. 1980). This difference between horizontal and vertical spatial scales can account for the fact that phytoplankton studies on horizontal heterogeneity focused on biomass, while those on vertical structure emphasized physiological properties. In addition, environmental characteristics are generally much more uniformly distributed on the horizontal than on the vertical. This is true for the two major proximal determinants of phytoplankton growth, light and nutrients (except areas of intense upwelling), which are both characterized by strong vertical gradients. Short-term vertical movements relative to those gradients can deeply affect phytoplankton growth, while short-term horizontal movements in the more homogeneous horizontal environment do not have the same drastic effects. It follows that temporal scales of variation do not have the same significance on the horizontal and vertical planes, which also helps to explain the different approaches to the horizontal and vertical phytoplankton structures. As long as uptake is considered (photosynthetic assimilation by phytoplankton and grazing by zooplankton or fish larvae), the above reasoning can be applied mutatis mutandis to zooplankton and fish larvae, since uptake is the vector through which significant scales are transferred from one trophic level to the next.

This discussion of spatial and temporal scales also explains why vertical studies are generally structured in the temporal dimension and horizontal investigations are not. Rate processes (physiology) respond much more rapidly to environmental changes than state variables (biomass), so that the former cannot be studied independently from the time axis, while the latter are more structured in space than in time. This is confirmed by the fact that horizontal studies on rate processes were never conducted without reference to the temporal dimension (see, e.g., Platt and Filion 1973; Therriault et al. 1978; Therriault and Platt 1981).

Sampling Techniques and Sampling Scales

There was a coevolution in the last decade of concepts and instrumentation in biological oceanography, which was recently reviewed by Herman and Platt (1980). The trend was towards instruments that could resolve fine spatial or temporal scales and generate long series of observations. In phytoplankton research, most of the present technology is based on in vivo fluorometry, either to estimate biomass (Lorenzen 1966) or, eventually, physiological rates (Samuelsson and Öquist 1977; Harris 1978; Roy and Legendre 1980). In zooplankton research, high-frequency echo-sounding (McNaught 1968), in situ electronic particle counting (Boyd 1973), and multiple opening and closing nets (Wiebe et al. 1976a; Sameoto et al. 1980) were used for biomass determinations.

These technological improvements and the oceanographic or limnological problems they allowed to be tackled led to new sampling strategies and equipment. The most significant developments concern the vertical dimension. Acoustic methods (high-frequency echo-sounder) can be used to record the vertical distribution of zooplankton along a transect or at an anchor station, without providing, however, simultaneous measurements of physical and/or chemical environmental variables.

To collect zooplankton samples and simultaneously record environmental variables, two modified versions of the Hardy (1936) continuous plankton recorder were developed: the Longhurst–Hardy plankton recorder (Longhurst and Williams 1976) and the undulating oceanographic recorder (Bruce and Aiken 1975), the latter being incorporated in a vehicle that could be preset to sample in an undulating or sawtooth pattern. Similarly, the "batfish" vehicle (Dessureault 1976) can be towed in a sawtooth pattern, but under shipboard command. It is capable of measuring environmental variables and in vivo fluorescence (Herman and Denman 1977), and it was also equipped (Herman and Dauphinee 1980) with the in situ electronic zooplankton counter (see above). All these were designed to study the vertical structure along a transect. To record time series of vertical profiles at an anchor or a drifting station, several laboratories are now developing automatic yo-yo profilers.

There are complex interactions between the physical and biological scales discussed above and the observational scale. Some unexpected interactions, such as aliasing, have already been examined, but the full impact of the physical and biological scales (Table 2) on the sampling design is still to be discussed.

On a given scale, one can observe simultaneously several hydrodynamic processes and therefore several biological responses. The biological responses that can be determined statistically correspond to all the environmental stimuli with a period shorter than half the length of the data series. For example, if the series is 50 h long, it should be theoretically possible to measure phytoplankton responses to the following environmental stimuli, given in order of increasing periodicities: wind-driven surface waves, small-scale turbulence, cloud cover, Langmuir circulation, M_4, M_2, and O_1 tidal harmonics, and the circadian light cycle. However, the biological responses that are actually observed depend on the frequency and design of the sampling.

Furthermore, the physical and biological characteristics for which changes can be shown at a given scale are only those whose periodicity is lower than half the length of the series. For example, if the series of observations is 7 d long, changes in phytoplankton properties may be shown for the photosynthetic characteristics, the nutrient uptake, the chlorophyll synthesis, and the growth rates but unlikely for the species composition (see fig. 1 in Harris 1980a; Table 2).

Finally, at a given observation scale, the living organisms respond directly to the environmental stimuli that occur on the same scale and indirectly to stimuli with a shorter periodicity. Such indirect responses result from the collapsing of short-term processes into longer term responses, as discussed by Harris (1980a). For example, changes in the community structure of phytoplankton observed on a seasonal scale (Table 2) may result from changes in growth rates that occurred on the scale of a few days.

A speculative example (Legendre et al. 1982b) will be used to summarize the complex interactions between the physical, biological, and observational scales. Let us assume that rapid light fluctuations (1-s periodicity) are continuously imposed on a phytoplankton population previously growing under stable light conditions. Some enzyme reactions in the photosynthetic apparatus would probably respond rapidly to the high-frequency stimulus (Gross and Chabot 1979; Walsh and Legendre 1982). Then within a few hours, the photosynthetic efficiency (α) would change, followed by changes in the photosynthetic capacity ($P^B_{\max}$) and in the pigment system (Walsh and Legendre 1982, 1983). After a few days, the growth rates of the various species would be differentially affected (Walsh and Legendre 1982), which would ultimately lead, in a few weeks' time, to changes in community structure. This speculative example is consistent with the opinion of Harris (1980a) that species composition may be controlled by high-frequency components of the environment. With a longer data series, it is thus theoretically possible to show a larger number of phytoplankton responses (starting here with enzyme changes and ending up with community changes); however, observing a given response requires appropriate sampling frequency or design.

These considerations on sampling scales probably apply to zooplankton and fish larvae as well. The main difference would be a change in the proximal determinants (for the phytoplankton: light and nutrients). When herbivorous grazers are considered, the proximal determinants include phytoplankton, and when it is carnivores, the proximal determinants include small zooplankton. This discussion of scales stresses the need for innovative critical sampling designs for investigating the developing hypotheses of dynamic biological oceanography and limnology.

Forthcoming Developments in Dynamic Biological Oceanography and Limnology

The previous section on current trends in dynamic biological oceanography and limnology mainly dealt with the physical and biological scales in the aquatic environment and the added complexity that is caused by the interaction between the observational scale and the natural scales (see also Haury et al. 1978). Anticipated developments in the next few years concern these same two topics, i.e. (1) the merging of the horizontal and vertical studies in an integrated approach to the aquatic ecosystems and (2) the design of new sampling techniques and schemes to probe the significant scales of variation in dynamic biological oceanography and limnology.

Horizontal–Vertical Continuum

It was explained in the previous section why phytoplankton studies on horizontal patchiness focused on state variables in the last decade, while those on the vertical structure emphasized rate variables. It is our view that the distinction between studies on the horizontal and vertical axes is not really justified and that careful consideration of phytoplankton responses to hydrodynamics will eventually succeed in merging the two approaches into a single conceptual model.

Numerical models of horizontal phytoplankton patchiness

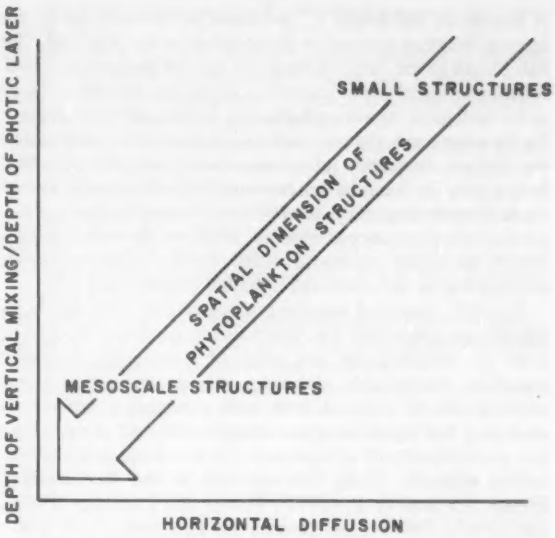
(KISS model and derived versions, see above) most often consider phytoplankton growth and hydrodynamics as two independent variables that oppose each other to produce (biological) or dissipate (physical) phytoplankton structures. This is also true of the three-dimensional extension of the KISS model (Platt and Denman 1975). However, contrary to this basic assumption of most models, studies on vertical dynamics have shown that phytoplankton growth is controlled by hydrodynamics, so that the two variables are not independent when the vertical dimension is taken into consideration. An integrated horizontal–vertical model of phytoplankton dynamics would therefore use, as forcing functions, the hydrodynamic processes that occur on the various horizontal and vertical scales and not growth rate, since it responds to the vertical hydrodynamics. A simple example for this approach is given in Fig. 4. When phytoplankton is vertically mixed to a depth that is large relative to the photic layer, the resulting photosynthetic rate is low, since phytoplankton responds to the average illumination in the deep mixed layer. This could happen, for instance, under conditions of high winds or strong tides, which would also lead to large horizontal diffusion. The combination of reduced growth and increased horizontal diffusion would result in small-scale phytoplankton patches. On the contrary, if the cells are vertically mixed to a depth that does not exceed the photic layer (resulting in high photosynthetic rate) and horizontal diffusion is moderate, a wider range of phytoplankton patches will be observed. Finally, on horizontal scales of 10–100 km, both horizontal diffusion and vertical mixing are small relative to the mesoscale water motions, so that phytoplankton distribution on these scales is almost independent from vertical processes.

The basic argument behind Fig. 4 is that phytoplankton dynamics are not controlled by a combination of various factors that include hydrodynamics but rather that a combination of several hydrodynamic processes, acting on different spatial and/or temporal scales, actually drive the dynamics of aquatic ecosystems. The actual implementation of such an idea into operational models requires a number of primary studies, both in the laboratory and in the field, on the biological responses to hydrodynamic processes. For phytoplankton, these responses may be direct or through the proximal agency of mainly light and nutrients. For zooplankton and fish larvae, the responses may also be direct, or through the proximal agency of, among other environmental factors, food, which includes phytoplankton (for the grazers) and smaller zooplankton (for the carnivores). In the context of dynamic biological oceanography or limnology, studies on biological responses to proximal agents must always be conducted with respect to hydrodynamics and therefore be properly scaled in both space and time.

Sampling Techniques and Designs

Studying biological responses to hydrodynamic processes implies that (1) the right biological property is observed on the right scale, (2) there exists a technique to measure this property in the aquatic environment, and (3) the sampling design is appropriate for the scale at which this property actually varies. These topics require new developments in the coming years.

In biological oceanography and limnology, the number of biological properties measured is most often exceedingly small. In many instances, sampling is limited to such state variables as numbers or biomass, despite the fact that rate properties are the only ones expected to vary on a number of ecologically important scales. That would be the same as if physical oceanographers were measuring only temperature and salinity.



DEPTH OF VERTICAL MIXING/DEPTH OF PHOTIC LAYER
SMALL STRUCTURES
SPATIAL DIMENSION OF PHYTOPLANKTON STRUCTURES
MESOSCALE STRUCTURES
HORIZONTAL DIFFUSION

FIG. 4. Spatial dimension of phytoplankton structures resulting from the combined action of horizontal and vertical hydrodynamics.

Among the biological rate properties, the most significant ones are probably the uptake rates. For phytoplankton, it is the photosynthetic rate; for herbivores, it is the grazing rate; for carnivores, it is the predation rate. As mentioned earlier, the importance of uptake rates lies in the fact that spatial or temporal heterogeneities can be transmitted to the next trophic level through the vector of uptake.

The reasons why biological rate properties are left out of several sampling programs are that (1) most of them are not easy to measure and (2) variations of these properties are often difficult to interpret in relation to such standard measured environmental variables as temperature and salinity. Despite technical difficulties, biological rates must and can be measured in the field within the framework of intensive sampling programs. It must be emphasized that the efforts invested in such programs bear fruit only if proper hydrodynamic and biological variables are measured simultaneously, the former being physical rate variables if the study concerns biological rates. In many instances, the intensive measurement of biological rates in the field can be made less cumbersome by giving up some of the precision that is achievable in the laboratory, since series analysis deals with variances and not with individual measurements. In some cases, "compromise" field methods may even improve on their laboratory ancestors, such as the photosynthetron (Lewis and Smith 1983) developed to rapidly measure photosynthesis–irradiance relationships. The ideal would be, however, to develop indices of biological rates simpler to measure than the rates themselves. For example, Harris (1978) suggested that in situ fluorescence compared with that of dark-adapted samples might be used as a rapid and simple indicator of potential phytoplankton productivity. Similarly, digestive enzymes have been suggested as indices of grazing rate (see above). Perfecting such physiological indices is a major task for the coming years.

Finally, successful studies linking biological responses to hydrodynamic processes cannot be conducted without considering the constraints imposed on the ecological interpretation by the design of the sampling scheme. The observational window is limited by the length of the series at one end and by the interval between successive observations at the other end. The half length of the series determines the environmental stimuli for which a direct biological effect can be demonstrated, as well as the biological responses that can be shown (previous section). On the other hand, the interval between successive samples sets the highest frequency of environmental stimuli for which biological effects can be demonstrated. This frequency, known as the Nyquist frequency, is equal to $(2 \times \text{sampling interval})^{-1}$. Outside the observational window, in theory, the environmental effects on living organisms either remain unknown (lower frequencies) or are confounded (higher frequencies).

Carefully designed sampling schemes may give access to frequencies lower than the observational window. This can be done by sampling the two sides of a temporal or spatial transition. Large-scale properties outside the observational window can be inferred from such a sampling scheme by assuming that rapid biological changes observed at the transition are indicative of a response to the low-frequency environmental stimulus. Using this approach in the St. Lawrence Estuary, Demers et al. (1979), Fortier and Legendre (1979), Lafleur et al. (1979), and Demers and Legendre (1979, 1981) studied the M_f (13.7 d) variations in phytoplankton properties using 7-d series sampled at the neap-spring tidal transition. Large-scale spatial structures can be similarly studied by sampling the two sides of their margins.

On the other hand, it should also be possible to gain access to frequencies higher than the observational window. Using phytoplankton as an example, samples could be incubated under environmental conditions that would artificially fluctuate with frequencies higher than the Nyquist sampling frequency. Two assumptions are then made: the first is that the cells in the natural environment are acclimated to the prevailing environmental fluctuations, and the second is that the cells will show maximum responses (either positive or negative) for the artificial frequency that corresponds to the natural frequency to which they are acclimated. At the end of the incubation, if some phytoplankton characteristics are significantly different (higher or lower) at one of the incubation frequencies, it can be concluded that these characteristics were already responding in the natural environment to a similar fluctuation. Using a crude approximation of this scheme, Walsh and Legendre (1983) incubated phytoplankton from the St. Lawrence Estuary under blue and white, steady and fluctuating (2.5 Hz) illuminations. Fluctuating blue light resulted in higher photosynthetic efficiencies (α), which led to the conclusion that fluctuating blue light was probably near the environmental conditions experienced by the cells in their natural environment.

A single large sample can also be used to study endogenous periodicities phased on hydrodynamics. For example, using a large phytoplankton sample from the St. Lawrence Estuary, Auclair et al. (1982) demonstrated a 6-h endogenous periodicity in chlorophyll synthesis, corresponding to tidal-induced changes in the vertical stability of the water column. The assumption here is that any biological periodicity in the large sample that is phased on hydrodynamic periodicities occurring in the natural environment results from an endogenous phasing of the biological property on these hydrodynamic variations.

The above sampling schemes were derived from the authors' first-hand experience with phytoplankton and given as examples of the kind of sampling strategies that can be used in dynamic biological oceanography and limnology. Such sampling designs are very different from those that have been traditionally used in aquatic ecology. New sampling strategies are needed to investigate the spatiotemporal and tridimensional variability of the aquatic environment. Designing such sampling schemes well adapted to the various trophic levels is a responsibility of biological oceanographers and limnologists.

In conclusion, dynamic biological oceanography and limnology is a new discipline that is emerging from a growing number of studies conducted on phytoplankton, zooplankton, and fish larvae. We think that the development of this new discipline is now irreversible, since it links biological processes to those of dynamic physical oceanography and limnology. We believe, however, that the pace of this development can be greatly increased if those involved in it realize that they have indeed entered a new discipline and if they agree on some common lines of research, such as those suggested above.

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Alteration of Fish Communities in Lakes Stressed by Acid Deposition and Heavy Metals near Wawa, Ontario

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Somers, K. M., and H. H. Harvey. 1984. Alteration of fish communities in lakes stressed by acid deposition and heavy metals near Wawa, Ontario. Can. J. Fish. Aquat. Sci. 41: 20–29.

Based on chemical criteria such as excess sulfate and low bicarbonate relative to cation, 50 lakes in the Wawa area show some degree of acidification. We conclude that the observed perturbations of lake chemistry and fish populations were primarily the result of smelting operations in the Wawa area. Six lakes have acidified to pH 3.1–4.1 and had high concentrations of metals such as Al, Mn, and Fe. Most of the lakes were in contact with felsic and mafic metavolcanic rocks containing minerals such as siderite, and only a few lakes had granitic basins. The six most acidic lakes contained no fishes and some lakes in the fume-kill area had known losses of brook trout (*Salvelinus fontinalis*) and lake trout (*Salvelinus namaycush*) populations. Based on a regression of number of species on lake area for 34 lakes, it was estimated that 83 fish populations have been lost from 16 lakes. Fish community changes were difficult to assess due to the distributions of species in the four watersheds. The northern pike (*Esox lucius*)–walleye (*Stizostedion vitreum vitreum*)–yellow perch (*Perca flavescens*) community was found now to be present only in lakes distant from the source of emissions. The fish community with brook and/or lake trout as the top predator was the most affected.

D'après certains critères chimiques, tels qu'un excès de sulfates et une faible teneur en bicarbonates par rapport au cation, 50 lacs de la région de Wawa montrent divers degrés d'acidification. Nous concluons que les perturbations observées des caractéristiques chimiques et des populations de poissons des lacs résultent surtout d'opérations de fonderies dans cette région. Six lacs ont été acidifiés à des pH de 3.1–4,1 et contiennent de fortes concentrations de métaux tels que Al, Mn et Fe. La plupart des lacs sont en contact avec des roches métavolcaniques felsiques et mafiques contenant des minéraux tels que la sidérite, alors que seulement quelques lacs possèdent des bassins granitiques. Les six lacs les plus acides ne contiennent aucun poisson, et certains lacs, dans la zone de mortalités par les émanations, ont perdu leurs populations d'ombles de fontaine (*Salvelinus fontinalis*) et de touladis (*Salvelinus namaycush*). On estime, par régression du nombre d'espèces sur la superficie de 34 lacs, que 83 populations de poissons sont disparues de 16 lacs. Il a été difficile d'évaluer les changements qui se sont produits dans les populations de poissons, à cause de la répartition des espèces dans quatre bassins hydrographiques. On constate que la communauté brochet (*Esox lucius*)–doré (*Stizostedion vitreum vitreum*)–perchaude (*Perca flavescens*) n'est présente que dans les lacs éloignés de la source d'émissions. La communauté de poissons ayant comme prédateurs supérieurs l'omble de fontaine ou le touladi, ou les deux, est celle qui est la plus affectée.

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This report describes a 2-yr study, 1978–79, of the fish communities of 50 lakes located at varying distances from a large point source of SO_2 and metal emissions. The north shore of Lake Superior is a region of moderately low acid loading via long-range transport of atmospheric pollutants (Whelpdale in Harvey et al. 1981), lying close to the isopleth of pH 4.7 for the annual weighted average pH of precipitation. The pH 4.7 isopleth marks the "threshold" below which adverse ecological effects occur in the most sensitive waters (Wright 1983a). Within this region, the area northeast of Wawa has been impacted severely by acid and metal deposition of local origin (Gordon and Gorham 1963; Stinnissen 1975; McGovern 1975). A study by the Ontario Ministry of Natural Resources revealed that several lakes in the terrestrial fume-kill had lost trout populations (Stinnissen 1975). This situation provided an opportunity to define the fish communities in a set of lakes along a gradient of acid loading and in an area including carbonate rock.

Study Area

The study area near Wawa is contained largely within the drainage basin of the Michipicoten River, comprising three major watersheds: Magpie River, Firesand Creek, and McVeigh Creek (Fig. 1). The 50 study lakes lie approximately along a transect extending northeast from the sintering plant. Half of the lakes are within 15 km of the emissions source and the remainder are up to 65 km distant.

In 1939 the Algoma Steel Corporation began open-pit mining of an extensive iron carbonate ridge near Wawa. A smelting process was employed to concentrate the siderite ore to a two-thirds Fe content (sinter) with SO_4 released as a by-product

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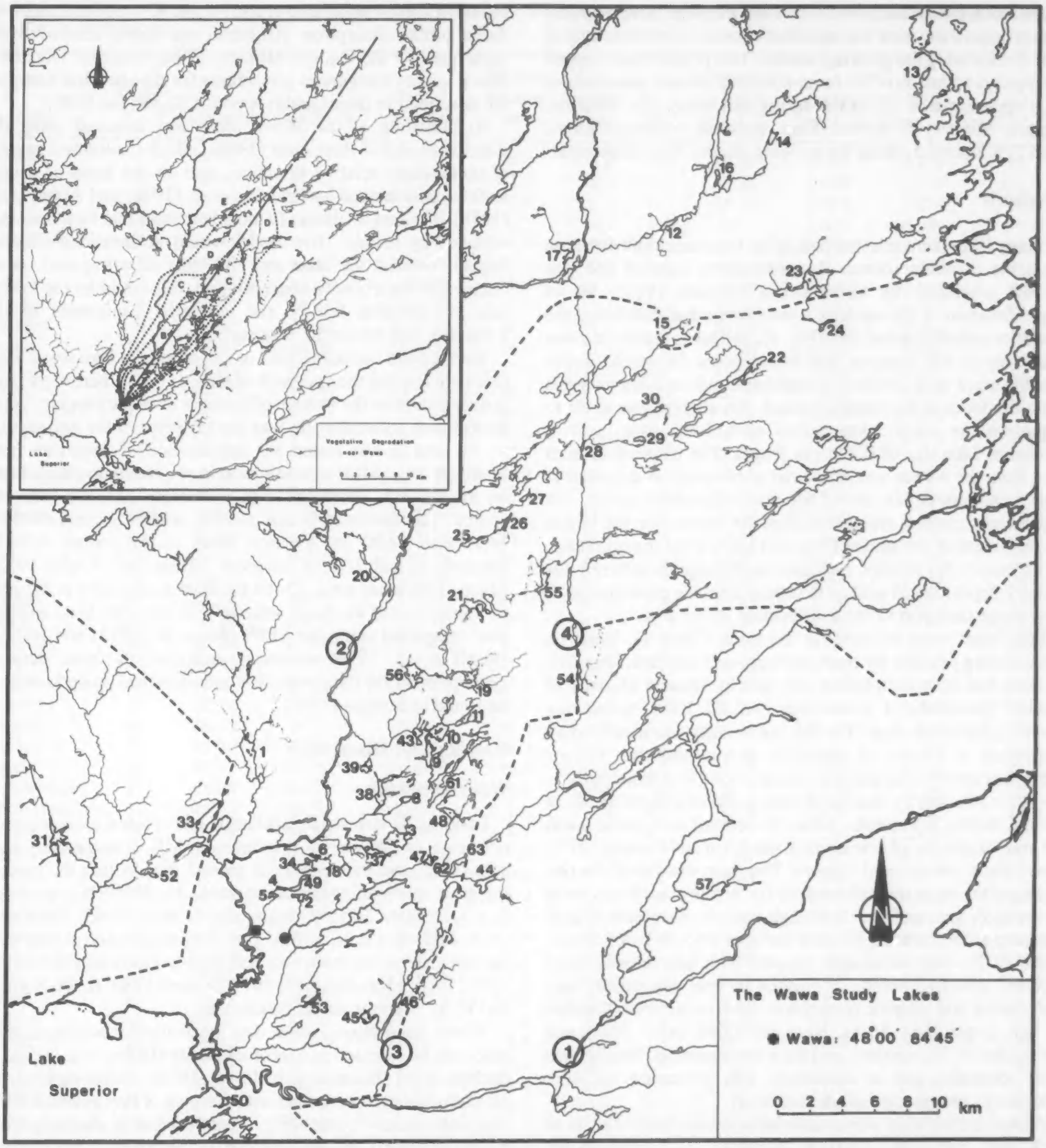
Vegetative Degradation near Wawa
0 2 4 6 8 10 Km
Lake Superior
A
B
C
D
E
13
14
16
12
17
23
15
24
22
30
29
28
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1
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39
9
61
38
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48
33
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34
18
37
13
47
62
63
44
52
4
49
5
2
57
53
45
46
3
1
50
Lake
Superior
The Wawa Study Lakes
Wawa: 48°00′ 84°45′
0 2 4 6 8 10 km

FIG. 1. Study area in relation to Wawa (●) and the sintering plant (■). Study lakes are identified by numbers (Table 1) within four major watersheds: (1) Michipicoten River, (2) Magpie River, (3) Firesand Creek, and (4) McVeigh Creek. Most lakes lay over bedrock containing carbonates (Precambrian felsic and mafic metavolcanics), as enclosed by the broken lines, with the remainder on granitic bedrock. Inset: distribution of vegetation damage as defined by Gordan and Gorham (1963): A, very severe; B, severe; C, considerable; D, moderate; E, not obvious.

of the burning of iron pyrites. Mining activities expanded in 1949, 1954, and 1958 with the discovery of underground deposits of high-quality ore with a reduced content of S and As. The open-pit mines were abandoned in favor of these underground Fe reserves.

The SO_2 fumigations and associated acid precipitation have transformed approximately 900 km^2 of the local birch, spruce, and pine forests into a severely damaged, fume-kill zone. Gordon and Gorham (1963) mapped the region impacted by the SO_2 emissions according to the severity of defoliation and subsequent erosion (Fig. 1). The patterns recorded at that time were confirmed by Stinnissen (1975) and comparable conditions were observed during this study. Concurrent erosion and occasional fires have further reduced the fume-kill core to barren rock (Stinnissen 1975). In 1962 the vegetative degradation prompted the mine management to switch to the smelting of low-S ore during the growing season. This practice has stopped the yearly expansion of the fume-kill zone. Annual emissions of SO_2 approximated 225 000 t during this study (D. Balsillie, Ontario Ministry of Environment, personal communication), with 27% liberated during the growing season, May–September.

Methods

Study lakes were selected in relation to distance and direction from the emission source. A northeasterly transect line was plotted originally by Gordon and Gorham (1963) as an approximation of the summer wind pattern that distributed the fumes over the impacted area (Fig. 1), and lakes that lay in close proximity to this transect line were chosen for study. Topographic maps were divided by concentric radii at 5-km intervals from the focus at the sintering plant. An attempt was made to apportion the study lakes across each 5-km zone, with a minimum lake size of 0.8 km in length. The distance of each lake from the source was measured as chimney to the point of lake maximum depth, site of the water chemistry station. No satisfactory method was established to correct for the lateral displacement of peripheral fume-kill lakes from the northeasterly transect. No attempt was made to distinguish between wet and dry deposition of acid or to separate out the contribution of long-range transport to the acidification of the area.

Fifty lakes were selected for the study (Table 1), based on access being possible by road, portage, or floatplane. One-half of these had been sampled or surveyed by Ontario Ministry of Natural Resources at some time, but 25 lakes lacked any previous documentation. The fish community was identified by employing a variety of sampling gear within the various habitats: experimental gill nets (composed of 8-m panels of 12-, 19-, 25-, 38-, and 51-mm mesh plus a second gill net of 64- or 76-mm mesh), fine mesh (1-mm fly screen) and coarse-mesh (51-mm) trap nets, plastic traps (Casselman and Harvey 1973), baited traps, seines, and dipnets. The gear was fished for one night and the catch was subsampled for 50 fish of each species to record size, sex, and age. Although random placement of gear has been recommended for such surveys (Moyle 1949; Southwood 1978), time constraints coupled with lake heterogeneity required selective netting. To assist in gear placement, lake bathymetry and edaphic parameters were considered. Catches of fish larger than 15 cm were identified (after Scott and Crossman 1973), counted, and their size recorded. Smaller fish were identified and a subsample was preserved for later laboratory confirmation of identification.

A chemistry station was established over the deepest basin of each lake. For ligand analysis, duplicate, 1-L surface-water samples (0.5-m depth) were collected in acid-washed, distilled water rinsed glass bottles. An additional 250-mL sample of surface water was collected in an acid-rinsed polyethylene bottle and acidified with 5 mL of nitric acid. Depth profiles were made for temperature (thermistor thermometer) and dissolved O_2 (azide modification of Winkler method) and Secchi (20-cm disk diameter) depth was recorded.

At the field laboratory, pH and total inflection point alkalinity (Anonymous 1980) were determined once, usually within a few hours of collecting the sample. The ligands SO_4, NO_3, and Cl were analyzed by automated, continuous-flow colorimetric techniques. The metals Al, Fe, Mn, Ca, and Mg were determined by inductively coupled argon plasma (ICAP) source emission spectrophotometry, and Na and K were determined by flame atomic absorption. All metal and ligand analyses were performed by the Ontario Ministry of Environment (Rexdale, Ont.); quality assurances procedures for the chemical analyses are described in their Quality Control Report for 1980.

Acidification of the Wawa lakes was assessed using the titration model of Henriksen (1980), which identifies a paucity of bicarbonate relative to cation, and on the basis of excess sulfate, as described by Gjessing et al. (1976) and Almer et al. (1978). The loss of alkalinity model assumes that bicarbonate is replaced by sulfate. The model would be invalid if $CaSO_4/MgSO_4$ entered the lake and was thus superimposed on an unchanged bicarbonate concentration; this could be the case if acid precipitation fell on the terrestrial component of the watershed but not on the lake surface.

Background concentrations of major ions in lake water were calculated, using the approach of Green (1965), here regressing concentration on the inverse of distance from the smelter. Thus, background concentration was the intercept of the ordinate ($D = \infty$), and it was tested for significance of departure from intercept = 0. Sulfur concentration in air, and hence, deposition on the ground, decreases with increasing distance from the source. The Gaussian plume models predict S concentrations best using $1/D^2$ for location close to the source (tens of kilometres) and $1/D$ at distances farther out (Rodhe 1972). Much of the study area (20–65 km from source) lies in the zone of transition and we chose arbitrarily to use $1/D$. Data analysis was completed using the SPSS (Nie et al. 1975) and NTSYS (Rohlf et al. 1974) statistical packages. A more detailed description of the data collection and analytical procedures may be found in Somers (1980).

Results and Discussion

Water Chemistry

Large-scale terrestrial defoliation and erosion have occurred northeast of Wawa in response to SO_2 fumigations, acid deposition, and the occasional ground fire. Within the core of this area, acid loading has maintained lake pH levels in the range 3–4 for nearly 20 yr (Gordon and Gorham 1963; Stinnissen 1975; McIlveen et al. 1979). That the precipitation is very acid has been shown by both rain and snow collections (McGovern 1975, 1976; McIlveen et al. 1979; Somers 1980; K. M. Somers and H. H. Harvey, unpublished data).

Where trend-through-time data are available, acidification of lakes can be assessed as loss of alkalinity (Dillon et al. 1978) or decline in pH (Beamish and Harvey 1972). Thirty-eight of the 50 study lakes are in contact with bedrock of Precambrian felsic and mafic metavolcanics (Fig. 1) and ranged in alkalinity from 0.0 to 95.9 $\mathrm{mg \cdot L\ HCO_3^{-1}}$ (Table 1). Seven lakes are north of the metavolcanics: Rosa, North, South, Aloft, Chick, Sausage, and Barry (alkalinity range 0.5–40.7 $\mathrm{mg \cdot L\ HCO_3^{-1}}$), three are to the west: Molybdenite, Black Trout, and Wing (alkalinity range 0.0–8.8 $\mathrm{mg \cdot L\ HCO_3^{-1}}$), and two are to the east: Vanreek and Borzoi (alkalinity 11.2 and 12.4 $\mathrm{mg \cdot L\ HCO_3^{-1}}$). These lakes are mainly in granitic basins, but the wide range of alkalinity would imply appreciable amounts of carbonates in some of the watersheds. Six lakes were very acid (pH range 3.09–4.05), contained zero alkalinity, and showed the anomalous water chemistry of low pH coincident with high Ca and Mg concentration (Table 1). Molybdenite Lake at pH 5.0 and zero alkalinity was outside the fume-kill area, and it may not have acidified in recent decades. In the absence of time-trend data it is

TABLE 1. Name, location, date of survey, and principle physical and chemical attributes of the 50 Wawa study lakes (Gazateer names unless specified as local names).

Lake	Code No.	Latitude	Longitude	Survey commenced	Smelter distance (km)	Area (ha)	pH	Alkalinity as HCO_3 ($mg \cdot L^{-1}$)	Al ($mg \cdot L^{-1}$)	Mn ($mg \cdot L^{-1}$)	SO_4 ($mg \cdot L^{-1}$)
Catfish	1	48°06′	84°48′	26/5/78	9.4	156.6	6.9	19.39	0.150	0.014	10.5
Moran	2	48°01′	84°46′	29/5/78	2.9	18.3	7.6	38.96	0.440	0.117	392.0
Lena	3	48°03′	84°41′	2/6/78	9.8	91.5	7.3	35.24	0.070	0.011	22.0
Otter	4	48°02′	84°47′	6/6/78	2.3	6.4	3.1	0	5.430	6.381	55.0
Little Soulier	5	48°01′	84°47′	7/6/78	1.8	8.4	3.2	0	3.090	4.332	242.0
Mink	6	48°03′	84°45′	13/6/78	5.3	9.4	3.9	0	1.770	1.458	86.5
Arliss	7	48°03′	84°43′	15/6/78	7.9	61.1	6.9	14.88	0.080	0.036	29.0
Brooks	8	48°04′	84°41′	17/6/78	11.5	12.1	7.9	78.84	0.100	0.005	280.0
Bauldry	9	48°06′	84°39′	19/6/78	14.5	51.4	7.2	26.65	0.040	0.008	26.0
Goetz	10	48°07′	84°39′	24/6/78	16.0	71.1	7.6	33.48	0.050	0.008	32.0
Parks	11	48°07′	84°37′	28/6/78	17.6	31.5	7.4	21.22	0.060	0.027	35.0
Rosa	12	48°23′	84°28′	30/6/78	49.2	23.8	7.0	22.56	0.070	0.014	10.5
North (local)	13	48°27′	84°15′	3/7/78	64.6	23.8	6.1	0.50	0.060	0.009	3.5
South (local)	14	48°26′	84°23′	6/7/78	55.6	25.1	7.1	19.70	0.120	0.011	10.0
Aloft	15	48°18′	84°27′	10/7/78	42.7	106.1	7.5	18.23	0.060	0.010	14.5
Chick (local)	16	48°25′	84°25′	15/7/78	51.8	17.8	7.7	40.67	0.010	0.024	11.0
Sausage	17	48°22′	84°33′	16/7/78	43.7	57.9	7.2	24.21	0.130	0.009	12.0
Walbank	18	48°02′	84°44′	19/7/78	6.1	34.9	7.5	45.85	0.080	0.000	35.5
Andre	19	48°08′	84°37′	24/7/78	19.2	61.1	7.5	32.51	0.090	0.022	5.0
Eva	20	48°12′	84°42′	1/8/78	21.9	24.7	7.7	34.27	0.090	0.029	20.5
Big	21	48°11′	84°37′	3/8/78	23.2	66.7	7.2	11.59	0.090	0.023	26.5
Strobus	22	48°19′	84°24′	7/8/78	43.9	63.5	8.4	95.85	0.130	0.012	13.5
Barry	23	48°21′	84°20′	9/8/78	50.3	43.7	7.8	35.98	0.110	0.006	12.5
Loughlin	24	48°20′	84°20′	11/8/78	49.1	17.6	7.5	27.01	0.120	0.030	16.0
Perry	25	48°13′	84°37′	15/7/78	26.4	30.4	8.3	29.82	0.060	0.022	21.5
Selkirk	26	48°13′	84°36′	16/8/78	27.8	34.4	7.5	21.28	0.080	0.022	21.0
Doherty	27	48°14′	84°35′	21/8/78	29.5	10.3	7.2	28.17	0.090	0.046	25.5
Summit	28	48°16′	84°32′	23/8/78	34.4	6.8	7.3	24.21	0.140	0.550	56.0
Dobbs	29	48°16′	84°29′	24/8/78	36.4	16.5	7.5	36.58	0.080	0.028	39.0
Lovell	30	48°17′	84°28′	26/8/78	38.6	13.0	7.5	26.04	0.080	0.036	14.5
Molybdenite	31	48°03′	84°58′	31/8/78	13.2	93.6	5.0	0	0.370	0.100	9.0
Black Trout	33	48°03′	84°50′	6/6/79	7.0	178.4	6.0	8.78	0.190	0.042	11.0
Lagarde	34	48°03′	84°46′	9/6/79	4.1	53.2	4.1	0	2.280	2.420	96.0
Francis	37	48°03′	84°42′	16/6/79	7.9	25.8	7.2	25.85	0.090	0.011	18.5
Mildred	38	48°04′	84°41′	23/6/79	10.6	69.2	7.1	25.85	0.090	0.012	51.5
Blueberry	39	48°05′	84°43′	25/6/79	11.2	32.1	3.8	0	0.290	0.482	56.0
Josephine	43	48°07′	84°40′	4/7/79	15.1	30.4	7.3	31.65	0.140	0.010	28.5
Vanreek	44	48°02′	84°37′	9/7/79	13.8	50.3	7.0	11.22	0.170	0.004	13.0
Reed	45	47°57′	84°43′	15/7/79	8.6	34.6	7.4	29.82	0.090	0.008	10.5
Lyre	46	47°58′	84°41′	17/7/79	9.8	20.4	7.6	46.71	0.100	0.013	12.0
Owens	47	48°02′	84°39′	23/7/79	10.9	25.6	7.3	28.84	0.120	0.012	13.5
Sunrise	48	48°04′	84°39′	27/7/79	13.2	36.2	7.1	10.85	0.130	0.016	15.0
Talbot	49	48°02′	84°46′	29/7/79	3.1	24.0	3.3	0	3.680	3.710	187.0
Roller	50	47°55′	84°50′	2/8/79	11.2	18.2	7.6	53.11	0.070	0.014	12.0
Wing (local)	52	48°02′	84°53′	8/8/79	7.4	28.7	6.9	7.68	0.130	0.026	9.0
Ward	53	47°57′	84°45′	10/8/79	5.7	15.4	7.0	11.22	0.130	0.021	8.5
Wallace	54	48°08′	84°32′	13/8/79	22.2	27.0	7.6	44.82	0.100	0.042	24.0
Alden	55	48°12′	84°34′	16/8/79	27.0	43.9	7.2	13.29	0.100	0.016	21.5
West Andre	56	48°09′	84°40′	21/8/79	17.3	83.8	7.6	19.88	0.110	0.012	25.5
Borzoi	57	48°02′	84°26′	27/8/79	27.7	84.5	7.4	12.44	0.130	0.007	9.5

not known if the Wawa lakes have reached steady state or if alkalinity will decline in future in response to continued acid loading.

In the absence of a time series, acidification can be measured as excess sulfate (Gjessing et al. 1976; Almer et al. 1978), high concentrations of Ca plus Mg relative to alkalinity (Almer et al. 1978), or Ca plus Mg minus alkalinity in relation to sulfate (Dillon in Harvey et al. 1981). Henriksen (1980) described the acidification process as analogous to a large-scale titration and constructed a nomogram (Henriksen 1979) for the simple recognition of acidified lakes. For the Wawa lakes, preimpact sulfate concentrations are not known. Sulfate concentration was correlated negatively ($r^2 = 0.30$) (Table 2; Fig. 2) with distance from the smelter. The regression of sulfate concentration on the inverse of distance from lake to smelter yielded an intercept of $0.88 \; mg \cdot L^{-1}$, which was not significantly different from zero (Table 3). This sulfate concentration is low compared with $3.6 \; mg \cdot L^{-1}$ for the 102 ELA lakes (Beamish et al. 1976).

Table 2. Correlation matrix of selected water chemistry parameters and distance from the sintering plant (Pearson's product-moment correlation coefficients). $r = 0.279$ at $\alpha = 0.05$; $r = 0.361$ at $\alpha = 0.01$.

Variable	Al	Fe	Mn	Ca	Mg	SO_4	pH	Alkalinity
Al	1.000							
Fe	0.8566	1.000						
Mn	0.988	0.8188	1.000					
Ca	0.455	0.396	0.459	1.000				
Mg	0.369	0.281	0.346	0.666	1.000			
SO_4	0.377	0.144	0.368	0.710	0.852	1.000		
pH	−0.817	−0.627	−0.805	−0.124	−0.187	−0.294	1.000	
Alkalinity	−0.409	−0.322	−0.401	0.444	0.064	0.083	0.674	1.000
log (distance)	−0.610	−0.436	−0.590	−0.375	−0.461	−0.519	0.602	0.284

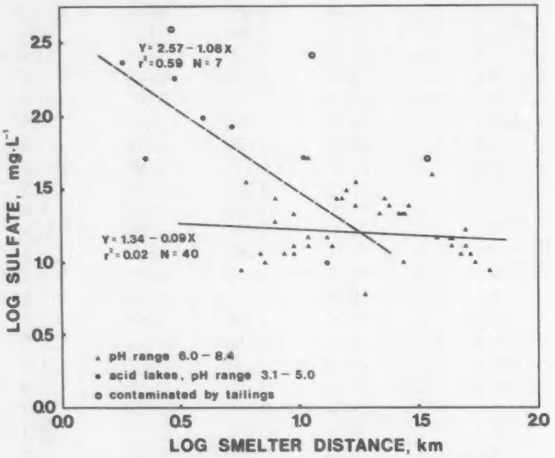

FIG. 2. Regressions of lake sulfate concentration on distance from the emissions source for seven acidified (●) and 40 nonacidified lakes (▲). Three lakes contaminated with mine tailings (○) were omitted from the regression.

Gordon and Gorham (1963) suggested that the prolonged loading of sulfuric acid had resulted in the leaching of both Ca and carbonates from the local soils to the extent that all buffering capacity in the central fume-kill lakes had been exhausted. This was based on their observations of reduced Ca and elevated acidity in small lakes nearest the sintering plant. McIlveen et al. (1979) came to the same conclusion from an examination of soil chemistry. There are now reports documenting unchanged, elevated, and decreased Ca in acidifying lakes (reviewed by Dillon in Harvey et al. 1981), possibly as a function of the stage of acidification. The watersheds from which such leaching measurements were made were noncalcareous, with carbonates largely restricted to surficial deposits. Thus, they are not readily comparable with the Wawa area of carbonate-bearing bedrock. In this study, both Ca and Mg concentrations were inversely correlated ($P < 0.01$) with distance from the smelter (Table 2). The six acid lakes showed significantly higher concentrations of Ca ($P < 0.01$) and Mg ($P < 0.01$) than the circumneutral lakes. Calculated background concentrations were Ca, $13.95\ mg \cdot L^{-1}$, which differed significantly from zero, and Mg, $-0.95\ mg \cdot L^{-1}$, not significantly different from zero. Thus, the acidified Wawa lakes have lost all bicarbonate, and acid loading is resulting in an ion-exchange yielding Ca plus Mg (Wright 1983b). The evidence that acid loading exceeds leaching capacity of Ca and Mg from the watersheds is the high concentration of H^+ and Al in lake water. In a plot of alkalinity against Ca plus Mg (as milliequivalents), all of the Wawa lakes fell below the 1:1 line, indicating substantially less alkalinity than expected (Dillon et al. 1980). The regression of sulfate on Ca plus Mg minus alkalinity yielded $Y = 0.986X - 89.1$, with $r^2 = 0.56$. Thus, sulfate was an essential component in charge balance and in the absence of increased leaching of Ca and Mg would approximate lost alkalinity. Plotted onto Henriksen's (1980) nomogram, three lakes fell in the acid category, two in the transition zone, and the remainder were bicarbonate lakes.

Aluminum concentration was much higher in the acid lakes (Fig. 3A). Because Al solubility is pH dependent, no regression was calculated for Al concentration on distance from the smelter. Calculated background concentration ($-0.334\ mg \cdot L^{-1}$) was not significantly different from zero (Table 3). Manganese solubility is also pH dependent (Fig. 3B), with pH more important than distance from the source of SO_2 in determining lake concentration, and thus the calculated background concentration for Mn was (an impossible) $-0.508\ mg \cdot L^{-1}$, significantly less than zero ($P < 0.05$). Iron concentration was correlated negatively ($r = -0.436$) (Table 2) with smelter distance. Background concentration (Table 3) was not significantly different from zero. At $D = \infty$, expected background concentrations for Al, Mn, and Fe were not greater than zero. It is concluded that the observed higher concentrations of the metals in lakes nearest the sintering plant were the direct result of the smelting activity. The mechanisms for this metal loading (atmospheric transport, terrestrial leaching, or recruitment from lake sediments) were not addressed in this study.

Loss of Fish Populations

The faunal surveys of the 50 lakes yielded 28 fish species (Table 4, Fig. 4). Seven lakes had no fish, and of these, only Brooks Lake was not acidified. Large quantities of Fe tailings with a high As content had been dumped into this lake from a nearby open-pit mine. It is possible that any former fish populations disappeared during these early mining activities. The remaining six fish-free lakes all had pH values below 5.0 (Table 1). Lagarde Lake once supported a large population of brook trout (*Salvelinus fontinalis*) (Stinnissen 1975), but no historical records could be found for the other five acid lakes. Based on an examination of early records and the results of this study, it was concluded that 12 populations of lake trout (*Salvelinus namaycush*) and brook trout had been lost from nine of the study lakes (Fig. 4). Some of the lakes laterally displaced from the severely damaged core area had reduced species

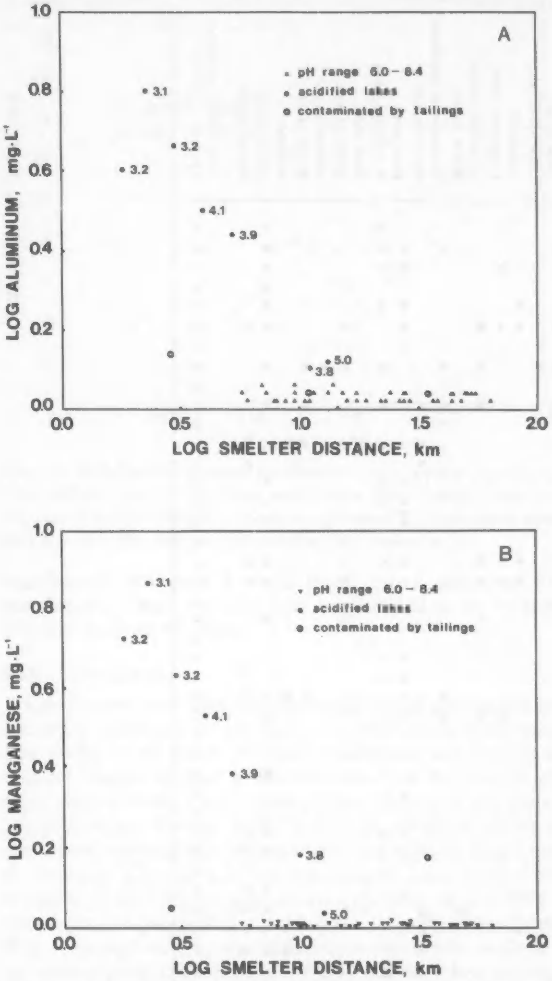

FIG. 3. Relationship between distance from SO_2 source and (A) lake Al concentration and (B) lake Mn concentration. Severely acidified lakes (●) have lake pH identified.

TABLE 3. Measured concentration vs calculated background concentration, plus significance of difference between the two, for six chemical variables in the 50-lake set (NS = not significant).

Variable	Measured ($mg \cdot L^{-1}$) Mean	Min.	Max.	Calculated background ($mg \cdot L^{-1}$)	Significance of t value
SO_4	44.1	3.5	392.0	0.88	NS
Ca	18.7	2.14	50.4	13.93	0.05
Mg	6.08	0.60	83.5	−0.95	NS
Al	0.43	0.04	5.43	−0.33	0.05
Mn	0.40	0.00	6.38	−0.51	0.05
Fe	0.39	0.00	9.04	−0.315	NS

TABLE 4. Frequency of occurrence of fishes in the Wawa area lakes.

Scientific name	Common name	No. of lakes	% of lakes
Catostomus commersoni	White sucker	36	72.0
Couesius plumbeus	Lake chub	31	62.0
Semotilus margarita	Pearl dace	23	46.0
Culaea inconstans	Brook stickleback	22	44.0
Chrosomus neogaeus	Finescale dace	21	42.0
Pimephales promelas	Fathead minnow	21	42.0
Chrosomus eos	Northern redbelly dace	20	40.0
Perca flavescens	Yellow perch	18	36.0
Etheostoma exile	Iowa darter	17	34.0
Salvelinus fontinalis	Brook trout	15	30.0
Rhinichthys cataractae	Longnose dace	10	20.0
Cottus cognatus	Slimy sculpin	10	20.0
Lota lota	Burbot	8	16.0
Esox lucius	Northern pike	8	16.0
Notropis cornutus	Common shiner	8	16.0
Notropis heterolepis	Blacknose shiner	7	14.0
Catostomus catostomus	Longnose sucker	7	14.0
Percina caprodes	Logperch	6	12.0
Stizostedion vitreum vitreum	Walleye	5	10.0
Salvelinus namaycush	Lake trout	5	10.0
Pungitius pungitius	Ninespine stickleback	5	10.0
Percopsis omiscomaycus	Trout-perch	4	8.0
Coregonus artedii	Lake herring	3	6.0
Coregonus clupeaformis	Lake whitefish	3	6.0
Notropis hudsonius	Spottail shiner	3	6.0
Notemigonus crysoleucas	Golden shiner	2	4.0
Notropis volucellus	Mimic shiner	1	2.0
Ambloplites rupestris	Rock bass	1	2.0

diversity when compared with previous records, such as Stinnissen (1975).

The number of fish species was correlated ($r^2 = 0.13$, $P < 0.05$) with the logarithm of the distance between the lakes and the smelter. Lake area has been shown to be a critical determinant of the number of fish species in a lake (Barbour and Brown 1974, for large lakes; Harvey 1978, 1981, for smaller lakes). Thus, lakes may be viewed as the analogues of islands in the area-diversity pattern of island biogeography as postulated by MacArthur and Wilson (1967). The implications of this analogous regulation of fish species diversity have been discussed by Magnuson (1976). In order to determine if lake size was a controlling variable, the lake set was divided into two halves, based on lakes smaller than 31 ha and greater than 31 ha, and again into halves closer than 15 km and farther than 15 km. The null hypothesis that the mean surface areas of the smaller lakes (close vs distant) were not significantly different was accepted on t-test, $t = 0.117$ ($t_{0.05} = 2.069$). The null hypothesis that the mean sizes of larger lakes (close vs distant) were not significantly different was also accepted, $t = 0.202$ ($t_{0.05} = 2.069$). Therefore, the increase in the number of species with increased distance from the source was not a function of lake size.

In order to estimate the prestress relationship between number of fish species and lake area, a subset of lakes was chosen from the original set of 50 lakes by eliminating three groups of lakes: (1) seven lakes currently without fish, (2) seven lakes with known species losses (Fig. 4), and (3) two lakes of large size (>40 ha) but lacking any of the large piscivorous fishes (lake trout, brook trout, northern pike (*Esox lucius*), walleye (*Stizostedion vitreum vitreum*), yellow perch (*Perca flavescens*), and burbot (*Lota lota*)) common to the area. No

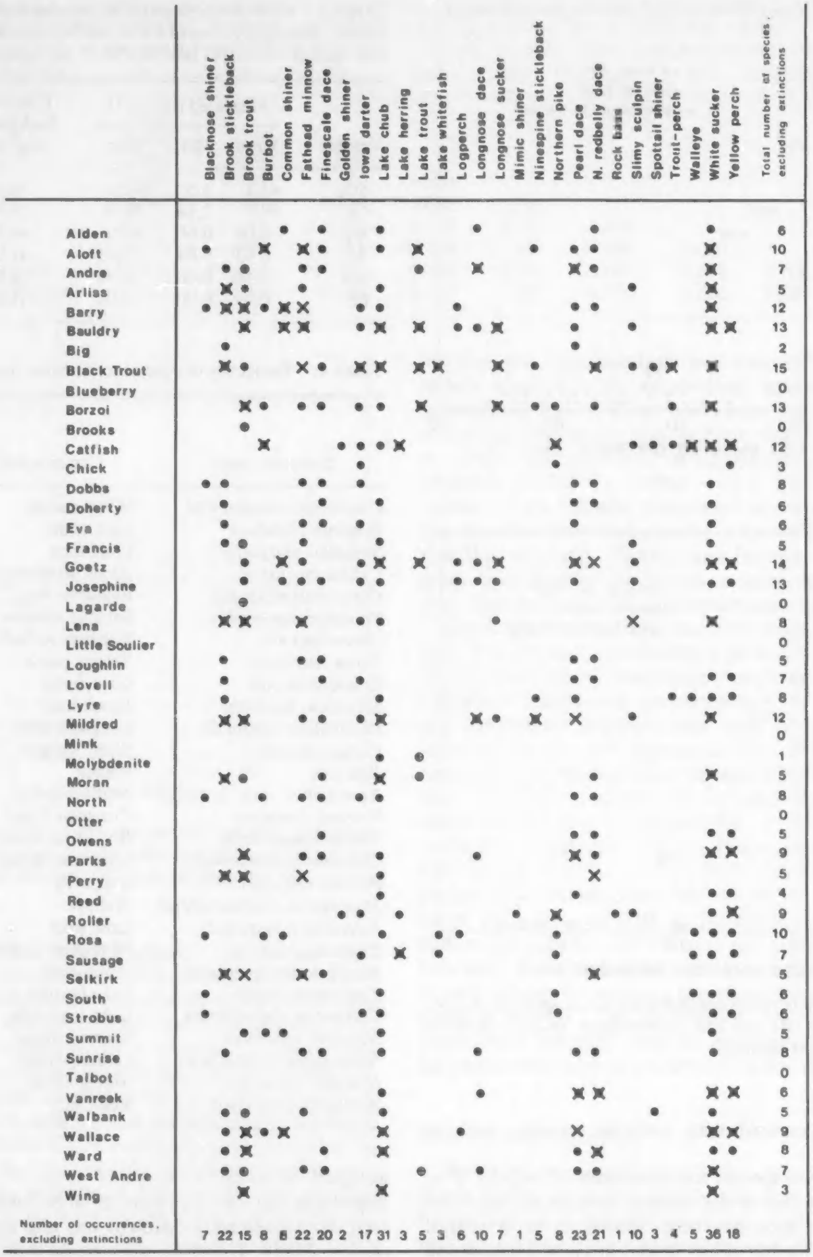
Blacknose shiner
Brook stickleback
Brook trout
Burbot
Common shiner
Fathead minnow
Finescale dace
Golden shiner
Iowa darter
Lake chub
Lake herring
Lake trout
Lake whitefish
Logperch
Longnose dace
Longnose sucker
Mimic shiner
Ninespine stickleback
Northern pike
Pearl dace
N. redbelly dace
Rock bass
Slimy sculpin
Spottail shiner
Trout-perch
Walleye
White sucker
Yellow perch
Total number of species, excluding extinctions
Alden 6
Aloft 10
Andre 7
Arliss 5
Barry 12
Bauldry 13
Big 2
Black Trout 15
Blueberry 0
Borzoi 13
Brooks 0
Catfish 12
Chick 3
Dobbs 8
Doherty 6
Eva 6
Francis 5
Goetz 14
Josephine 13
Lagarde 0
Lena 8
Little Soulier 0
Loughlin 5
Lovell 7
Lyre 8
Mildred 12
Mink 0
Molybdenite 1
Moran 5
North 8
Otter 0
Owens 5
Parks 9
Perry 5
Reed 4
Roller 9
Rosa 10
Sausage 7
Selkirk 5
South 6
Strobus 6
Summit 5
Sunrise 8
Talbot 0
Vanreek 6
Walbank 5
Wallace 9
Ward 8
West Andre 7
Wing 3
Number of occurrences, excluding extinctions
7 22 15 8 8 22 20 2 17 31 3 5 3 6 10 7 1 5 8 23 21 1 10 3 4 5 36 18

FIG. 4. Matrix of all available information on reported fish presence in the 50 study lakes: species found in this study (●), species reported in OMNR lake surveys (Stinnissen 1975) (×), occurrences recorded in OMNR files (○), species reported previously but not found in this study (+), plus three combinations of the above.

historical records are available for these two lakes, but the absence of top fish predators, the presence of old fishing camps, and location of the lakes within the central fume-kill led us to suspect the loss of some species.

For the seven fish-free lakes, the regression equation for number of fish species on log lake area (Fig. 5) yields 44 populations that would have been present, preimpact. For the seven lakes of known losses, the regression yields 63 populations, but only 35 were found for a deficit of 28 populations. The two lakes (No. 3 above) would be expected to contain 19

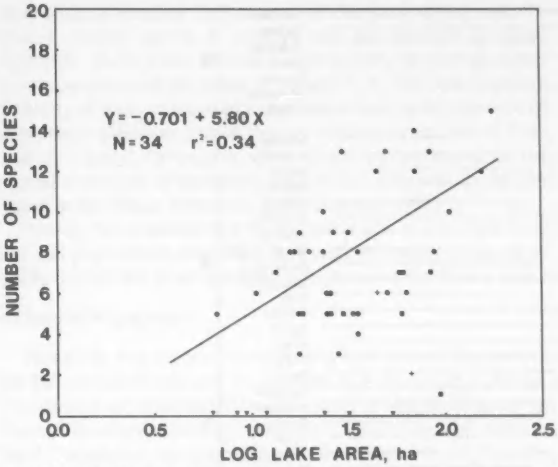

FIG. 5. Relationship between the number of fish species present and lake surface area for 34 of the study lakes (●). Omitted from the regression were seven lakes with no fish present (▼), seven lakes with partial losses (■), and two lakes lacking top predators (+).

populations, but only 8 were found for a deficit of 11 populations. Thus, the total loss is estimated to be 83 fish populations from 16 lakes.

Fish Communities

Lake groups were identified using a clustering algorithm with Jaccard's coefficient of similarity for fish presence–absence data (Rohlf et al. 1974). Jaccard's coefficient was employed because shared species omissions were not considered as significant as absence of a species from one lake of any given pair (Cairns and Kaesler 1969). Due to the nature of Jaccard's coefficient, lakes without fish (group 1) had to be omitted from the analysis. Clustering of the remaining 43 lakes yielded an hierarchy of lake groups (Fig. 6). At a phenetic value of 30%, two major groups resulted: (1) the seven lakes (Catfish–Chick (Fig. 6, group 6 below)) dominated by northern pike, walleye, and yellow perch (pike occurred in only one other lake outside this group and walleye occurred only in lakes of this group) and (2) a major cluster composed primarily of lakes in which either or both of brook trout or lake trout were present as the top predator. At a phenetic value near 33%, the latter cluster was composed of eight lake groups. Four of these groups (Big Lake, Molybdenite Lake, Lakes Summit + Wing, and Lakes Arliss + Francis + Walbank, collectively group 2) resulted from the extreme paucity of fishes. The next group comprised Lakes Lena–Wallace (group 5) and these were marked by the greatest diversity of fish species. One group, Vanreek + Reed + Lyre (group 3), resulted from the unusual species association white sucker (*Catostomus commersoni*) + yellow perch + lake chub (*Couesius plumbeus*) + pearl dace (*Semotilus margarita*). The largest group, lakes Moran to Selkirk (group 4), clustered primarily on similarity of cyprinids.

Cluster analysis was repeated on the 43 lakes, including as species present the known losses of six brook trout and four lake trout populations from these lakes. Lake groupings were altered slightly: Lakes Black Trout and Borzoi shifted due to the cooccurrence of both brook trout and lake trout; Lena Lake moved due to the cooccurrence of brook trout with Arliss, Francis, and Walbank.

The clustering technique was employed again to identify species assemblages based on site co-occurrences (Fig. 7). These associations were termed communities, where communities were defined according to Johnson et al. (1977) as a commonly occurring species group and identified by the top predator(s) where possible. At the first level of the fish dendrogram, rock bass (*Ambloplites rupestris*), mimic shiner (*Notropis volucellus*), golden shiner (*Notemigonus crysoleucas*), and lake herring (*Coregonus artedii*) were removed, as they occurred in only one or two lakes. Such rare occurrences have no contribution in defining associations across a large set of samples (Sneath and Sokal 1973). The frequently occurring white sucker also contributed little to the species groups, but was retained in the analysis. At a phenetic value of 15%, there were three major groups: (1) the northern pike + walleye + yellow perch association only found outside the central fume-kill, (2) the coldwater species of lake trout, ninespine stickleback (*Pungitius pungitius*), trout-perch (*Percopsis omiscomaycus*), and spottail shiner (*Notropis hudsonius*), and (3) an association consisting of the brook trout, two species of sucker, and several minnow species.

A further subdivision to a phenetic value of 25% similarity separated the rarer species such as the whitefish (*Coregonus clupeaformis*) and spottail shiner into separate groups. Burbot and the blacknose shiner (*Notropis heterolepis*) separated from the northern pike–walleye–yellow perch assemblage. The largest association divided into a lake trout assemblage, a cyprinid assemblage with no top predator, and a brook trout assemblage (Fig. 7). Repeating the cluster analysis with the inclusion of known losses of brook trout and lake trout populations, the assemblages did not change.

The six site groups (Fig. 6 plus lakes without fish), as defined by fish species associations, were compared for significance of differences between means for physical and chemical attributes (ANOVA, $P < 0.05$; Duncan's multiple range test, $\alpha = 0.05$). The fish-free lakes (group 1) were confined to the area immediately north of the source of emission. These lakes had significantly greater H^+, SO_4, Al, As, Ca, and conductivity and significantly less (zero) alkalinity and were significantly smaller in area but not different in mean or maximum depth. The seven lakes, Arliss–Big (group 2) containing very few species and with known losses of four trout populations, lie immediately adjacent to the acidified lakes. These seven lakes were significantly lower in alkalinity than the remaining four groups. Lakes Vanreek–Lyre (group 3), located south and east of the emissions source, were marked by the species association yellow perch + white sucker + lake chub + pearl dace. Alkalinity was relatively high (mean = 29.27 $mg \cdot L\ HCO_3{}^{-1}$) and sulfate was relatively low (mean = 12 $mg \cdot L^{-1}$). Thus, it was not apparent that the unusual species association that characterized this set of lakes was related to acid loading. Lakes Moran–Selkirk (group 4) may have been stressed, as evidenced by the loss of six populations of lake trout and brook trout and the low species diversity. These lakes extended northeasterly, approximately along the transect line extrapolated beyond the terrestrial effects (Fig. 1). Within this area were two of the more depauperate lakes. These lakes did not differ significantly in any physical–chemical attribute, but sulfate concentration at a mean of 41 $mg \cdot L^{-1}$ was very high and was exceeded only in group 1 lakes (mean = 119 $mg \cdot L^{-1}$). Lakes Lena–Wallace (group 5) showed the greatest diversity of fishes and were intermediate in distance from the emissions source but were significantly larger in area. The lakes of the upper Magpie River drainage (group 6)

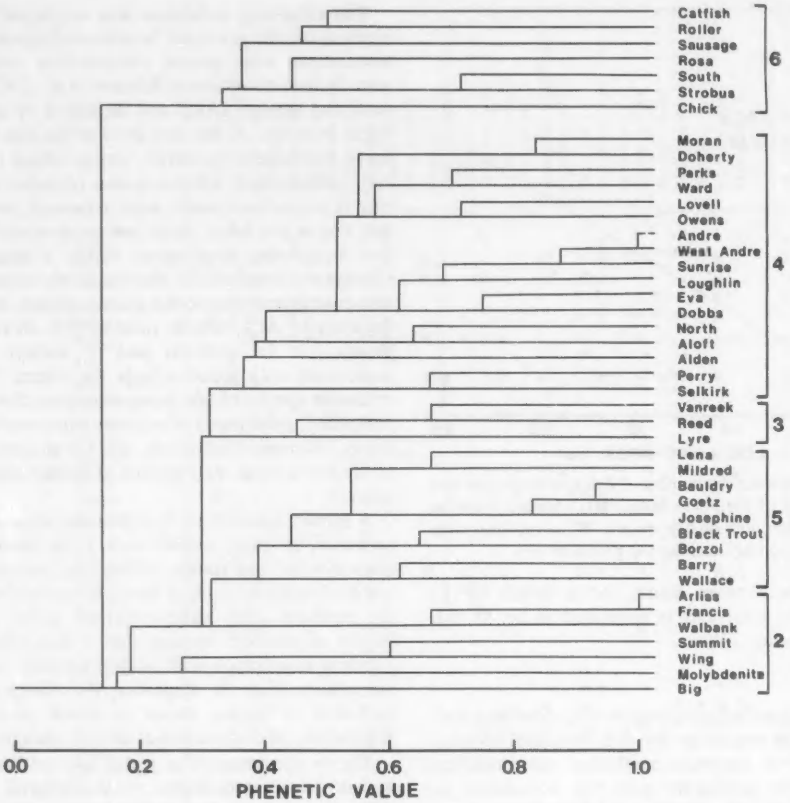

FIG. 6. Dendrogram of lake groupings based on UPGMA, Jaccard's coefficient of similarity, using fish presence–absence recorded in this study. Lakes with no fish present were omitted. Cophenetic correlation coefficient was 0.82. Numerals on the right refer to lake groups (group 1 is fishless lakes and does not cluster).

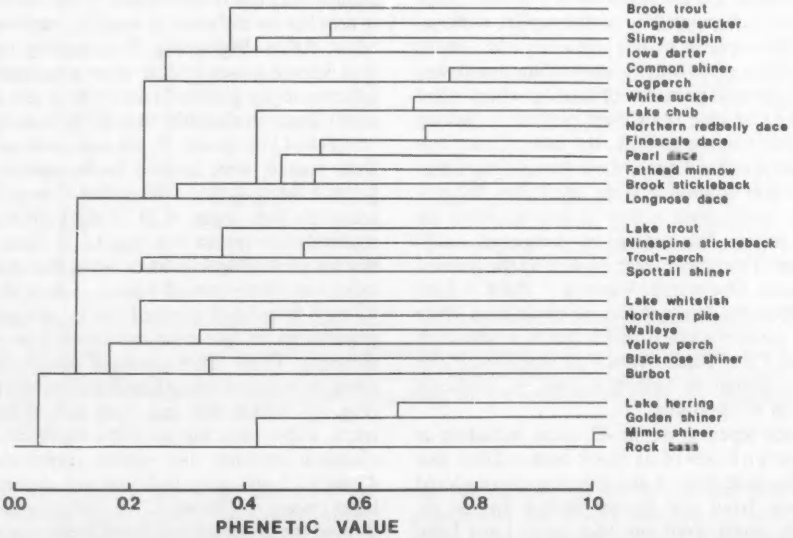

FIG. 7. Dendogram of species associations, cluster analysis, UPGMA, Jaccard's coefficient of similarity, based on fish presence–absence data from this study. Cophenetic correlation coefficient was 0.84.

were characterized by the presence of the piscivorous northern pike + yellow perch + walleye and the absence of many cyprinids. These lakes showed a significantly greater alkalinity in comparison with the lakes of groups 1–5. The lower species diversity of some of these lakes may be related to the presence of these three predators rather than to environmental stress from acid and metal deposition. This could be analogous to the mutual exclusion of northern pike and four cyprinid species, as found in the Bruce Peninsula lakes (Harvey 1981).

Overall, we conclude that the perturbations of lake chemistry and fish populations described here were primarily the result of acidic deposition from smelting operations in the Wawa area.

Acknowledgments

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Nutrient Regeneration in Deep Baffin Bay with Consequences for Measurements of the Conservative Tracer NO and Fossil Fuel CO_2 in the Oceans

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Jones, E. P., D. Dyrssen, and A. R. Coote. 1984. Nutrient regeneration in deep Baffin Bay with consequences for measurements of the conservative tracer NO and fossil fuel CO_2 in the oceans. Can. J. Fish. Aquat. Sci. 41: 30–35.

We found the nitrate to phosphate ratio of nutrients regenerated in Baffin Bay to be lower than is typical of most other ocean regions. The conservative tracers NO and PO are constant for water below 500 m providing NO and PO are redefined to account for this different nitrogen to phosphate ratio in the decaying organic matter of Baffin Bay. A modified stoichiometric model for decaying organic material in Baffin Bay was constructed based on measured values of carbonate, nitrate, and phosphate. A major difficulty in assessing the amount of fossil fuel CO_2 in the ocean is the determination of the amount of inorganic carbon produced during the decay of biogenic material. Using the modified stoichiometric model for decaying biogenic material, we show how regional and seasonal variations in the amount of carbon released and oxygen consumed during decay could be sufficiently different from what is predicted by the Redfield–Ketchum–Richards model to cause major differences in the assessment of the amount of fossil fuel CO_2 present in the water. The modified stoichiometric model offers the opportunity to determine the oxygen–carbon relationships more accurately and to obtain better estimates of fossil fuel CO_2 in the ocean.

On a constaté que le rapport nitrates–phosphates des substances nutritives régénérées dans la baie Baffin était inférieur aux rapports typiques de la plupart des autres régions océaniques. Les traceurs conservateurs NO et PO sont uniformes dans des eaux de profondeur supérieure à 500 m, pourvu qu'il n'y ait pas de NO ou de PO de redéfini pour expliquer ce rapport azote–phosphates différent dans la matière organique en décomposition de la baie Baffin. En nous fondant sur des valeurs mesurées de carbonates, nitrates et phosphates, nous avons construit un modèle stoïchiométrique modifié pour la matière organique en décomposition dans cette baie. La détermination de la quantité de carbone inorganique produite durant la décomposition du matériel biogénique pose un problème majeur dans l'évaluation de la quantité de CO_2 des combustibles fossiles dans l'océan. A l'aide de ce modèle, nous démontrons comment les variations régionales et saisonnières de la quantité de carbone mise en liberté et de l'oxygène consommé durant la décomposition pourraient être suffisamment différentes de ce que le modèle de Redfield–Ketchum–Richards prédit pour être le cause d'importants écarts dans l'évaluation des quantités de CO_2 de combustibles fossiles présents dans l'eau. Le modèle stoïchiométrique modifié permet de déterminer avec plus grande précision les relations oxygène–carbone et d'obtenir de meilleures estimations du CO_2 de combustibles fossiles dans l'océan.

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The regeneration of nutrients in the oceans has been described in terms of a stoichiometric model that relates constituents of biogenic material to resulting products when this material decays (Redfield et al. 1963). This Redfield–Ketchum–Richards relationship shows a certain constancy in the relative amounts of the constituents of biogenic material throughout the world's oceans, and as a result, has been used to help define a conservative tracer, "NO" (Broecker 1974). The concept of NO is based on the simultaneous utilization of oxygen and release of nitrate as biogenic material in the ocean decays. If the average relative amounts of carbon, oxygen, and nitrogen are the same in decaying biogenic material in the oceans, then the relative amount of oxygen consumed and nitrate produced will also be the same. For a given water mass, NO would then be determined by the amount of oxygen and nitrate present before decay occurs and by the relative amounts of carbon, nitrogen, and oxygen in the decaying biogenic material.

The concept of NO has been used to discuss water masses (Broecker 1974) and to help determine the amount of fossil fuel

CO_2 in the oceans (Brewer 1978; Jones and Levy 1981). In these studies and in many others, it was assumed that the Redfield–Ketchum–Richards relationship was an appropriate representation of the composition of decaying biogenic material.

We have examined nutrient regeneration in Baffin Bay in terms of NO and also in terms of the stoichiometric relationships among nutrients, oxygen, and carbon. We find that the stoichiometric composition of the biogenic material is different from that generally found elsewhere, and hence, a different relationship between oxygen and nitrate concentrations is required to construct a value for NO to characterize a conservative tracer for water masses in Baffin Bay.

The physical oceanography of Baffin Bay has been described by Muench (1971). Briefly, water enters Baffin Bay from the Arctic Ocean through the Canadian Archipelago and from the Labrador Sea via the West Greenland Current through the eastern part of Davis Strait. Water leaves Baffin Bay via the Baffinland (or Canadian) Current through the western part of Davis Strait. Muench (1971) described the water of Baffin Bay in terms of three layers. The upper layer, about 250 m deep, is primarily Arctic Ocean Surface Layer water, which is formed in the Arctic Ocean from North Atlantic and Bering Sea water. The intermediate layer, between about 250 and 1200 m, is North Atlantic water that has entered through Davis Strait. The deep layer, below 1200 m, is North Atlantic water from the Arctic Ocean that has pulsed through Nares Strait at irregular intervals and has a long residence time in Baffin Bay (Top et al. 1980). The water structure is quite homogeneous throughout Baffin Bay (Coote and Jones 1982).

Materials and Methods

Nutrients, oxygen, alkalinity, and total inorganic carbon have been measured at several locations in Baffin Bay. Details of the measurements and some of the data have been presented previously in different contexts (Jones and Coote 1980; Jones and Levy 1981; Coote and Jones 1982; Jones et al. 1983). Briefly, the analytical procedures were as follows. Nutrients were analyzed within a few hours of collection following standard methods (Strickland and Parsons 1968) using an AutoAnalyzer. Analytical precision was ±0.4 μmol/L for nitrate and silicate and ±0.02 μmol/L for phosphate. Accuracy was monitored with CSK standards and is believed to be within twice this range. Alkalinity and total inorganic carbon were measured using a semiautomated modification of the titrations method described by Dyrssen and Sillen (1967). Titrations were done within a few hours of sample collection in a closed cell at constant temperature (25°C). The resulting titration curve was analyzed using a curve-fitting procedure (Johansson and Wedborg 1982; Barron et al. 1983). The analytical precision was ±10 μmol/L for alkalinity and ±20 μmol/L for total inorganic carbon. Oxygen concentrations were measured following a modified Carpenter–Winkler technique (Levy et al. 1977) with an analytical precision of ±1 μmol/L. Salinity was measured with a Guildline Autosal model 8400 salinometer and temperatures were obtained from a Guildline Mk III analogue CTD system.

The data discussed in this paper were collected from six stations in Baffin Bay: station 12 (68°08.7′N, 61°21.3′W), station 13 (70°02.3′N, 62°46.1′W), station 17 (73°42.0′N, 64°34.9′W), station 18 (73°40.2′N, 67°17.3′W), station 19 (72°14.1′N, 65°56.9′W), and station 28 (73°42.0′N, 70°29.0′W) (Coote and Jones 1982).

Results and Discussion

The six stations chosen for this study range over much of central Baffin Bay and include the deepest regions. Composite profiles of data from all the stations are shown in Fig. 1. As can be seen, there is little difference among the data from each station contributing to the profiles, the scatter in the data often being not much greater than the precision of the measurements. The high degree of homogeneity of the water structure invites a detailed interpretation in terms of both physical and chemical parameters. In this paper, we confine ourselves to an examination of the chemical relationships among the data, both to comment on nutrient regeneration in general and to take one step towards a more complete understanding of the processes that determine the profiles.

Nutrient–Oxygen Relationships

We approach the question of nutrient regeneration in Baffin Bay by first examining the utilization of oxygen as biogenic material decays. This process is often represented by the Redfield–Ketchum–Richards relationships (Redfield et al. 1963), usually written in the form

$$\begin{aligned}(1)\quad & [(CH_2O)_{106}(NH_3)_{16}H_3PO_4] + 138[O_2] \\ & = 106[CO_2] + 122[H_2O] + 16[HNO_3] + [H_3PO_4].\end{aligned}$$

The nitrate regenerated in the water column during decay is proportional to the oxygen consumed, i.e.

$$(2)\quad [O_2]_{pre} - [O_2] = n\{[NO_3^-] - [NO_3^-]_{pre}\}$$

where the subscript indicates preformed values or values that would be present had decay not occurred and n is the constant of proportionality. From these relationships with $n = 9$, Broecker (1974) defined the conservative property NO as

$$(3)\quad \begin{aligned}NO &= [O_2]_{pre} + 9[NO_3^-]_{pre} \quad \text{or} \\ NO &= [O_2] + 9[NO_3^-].\end{aligned}$$

Since phosphate is released to the water at the same time as nitrate, Broecker (1974) defined a similar property, PO, as

$$(4)\quad \begin{aligned}PO &= [O_2]_{pre} + 135[PO_4^{3-}]_{pre} \quad \text{or} \\ PO &= [O_2] + 135[PO_4^{3-}].\end{aligned}$$

The values of NO and PO for a water mass are determined by the preformed values of nitrate, phosphate, and oxygen in the water when it was formed. The coefficients of $[NO_3^-]$ and $[PO_4^{3-}]$ are determined by the stoichiometric composition of the decaying organic matter.

Because the water in Baffin Bay below the upper layer is believed to have a common source in the North Atlantic, we expect that it should have a constant NO value. Also, the sedimentation rates are very low, of the order of a few millimetres per century, so that very little biogenic material should be buried and hence regenerated within the sediments. We therefore propose that a reasonable model for nutrient regeneration in Baffin Bay assumes that almost all regeneration occurs within the water column. This does not exclude regeneration at the water–sediment interface so long as the oxygen consumed by regeneration comes from the water column and that released nitrate and phosphate remain in the water column.

To explore this further, we examine the water column between 500 m, corresponding to the maximum value of the TS relationship (Coote and Jones 1982), and 1800 m. This excludes

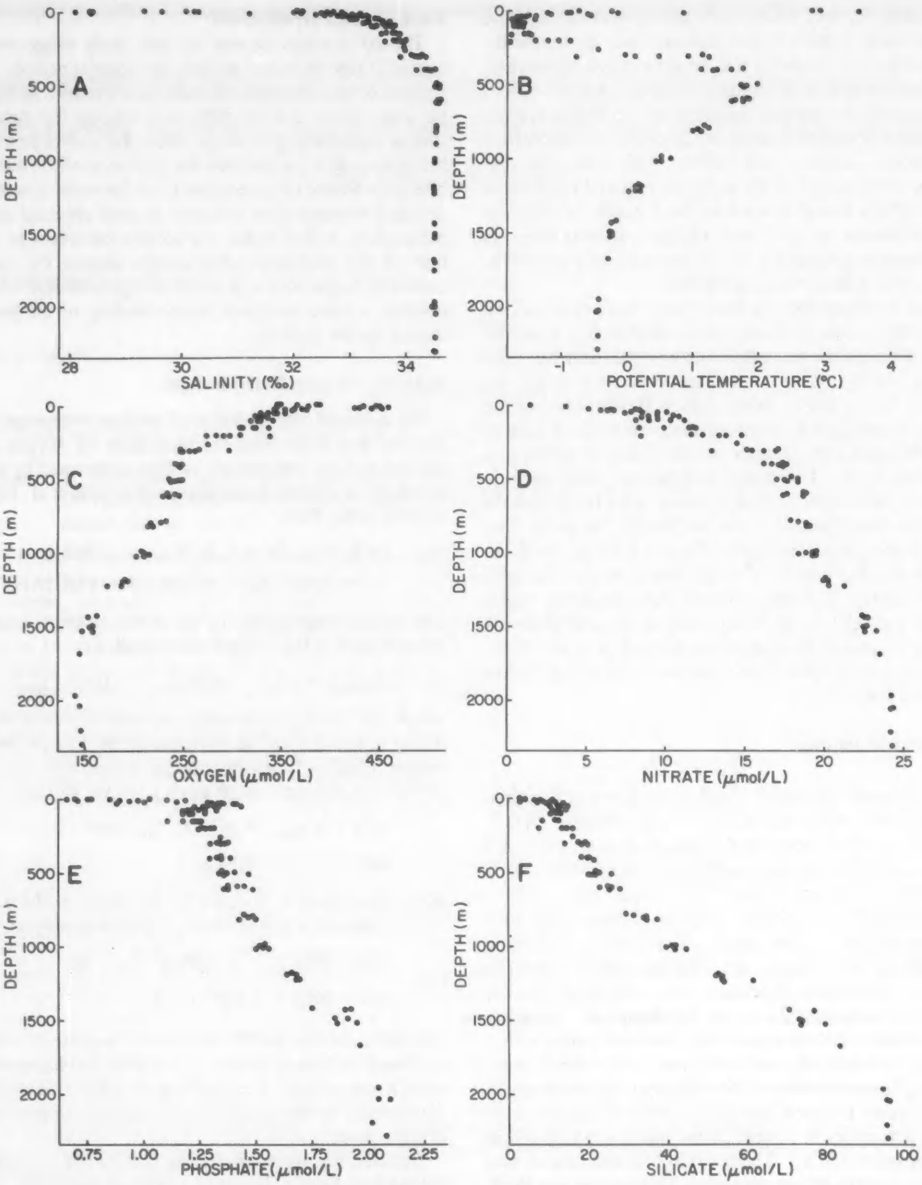

FIG. 1. Composite depth profiles of chemical quantities for Baffin Bay stations.

water above 500 m to avoid any mixing effects with the upper layer as well as water below 1800 m, the Baffin Bay Bottom water, to avoid small contributions from regeneration within the sediments. We find a very good linear fit of the $[O_2]$ vs $[NO_3^-]$ data (Fig. 2A) with the equation

$$(5)\quad [O_2] = -17.5[NO_3^-] + 549\ (r^2 = -0.98).$$

A similar fit of the $[O_2]$ and $[PO_4^{3-}]$ data (Fig. 2B) results in the equation

$$(6)\quad [O_2] = -168[PO_4^{3-}] + 470\ (r^2 = -0.97).$$

Thus, there is a linear relationship between $[O_2]$ and both $[NO_3^-]$ and $[PO_4^{3-}]$ as there should be if the water mass all has the same preformed values of nitrate, phosphate, and oxygen. The slope of the line for $[O_2]$ vs $[NO_3^-]$, however, is −17.5, much greater than −9 as predicted by the Redfield–Ketchum–Richards model. For $[O_2]$ vs $[PO_4^{3-}]$, the slope is −168 rather than −135. Written in the form of NO and PO, eq. 4 and 5 give

$$(7)\quad (NO)' = 549 = [O_2] + 17.5[NO_3^-]$$

and

$$(8)\quad (PO)' = 470 = [O_2] + 168[PO_3^{3-}].$$

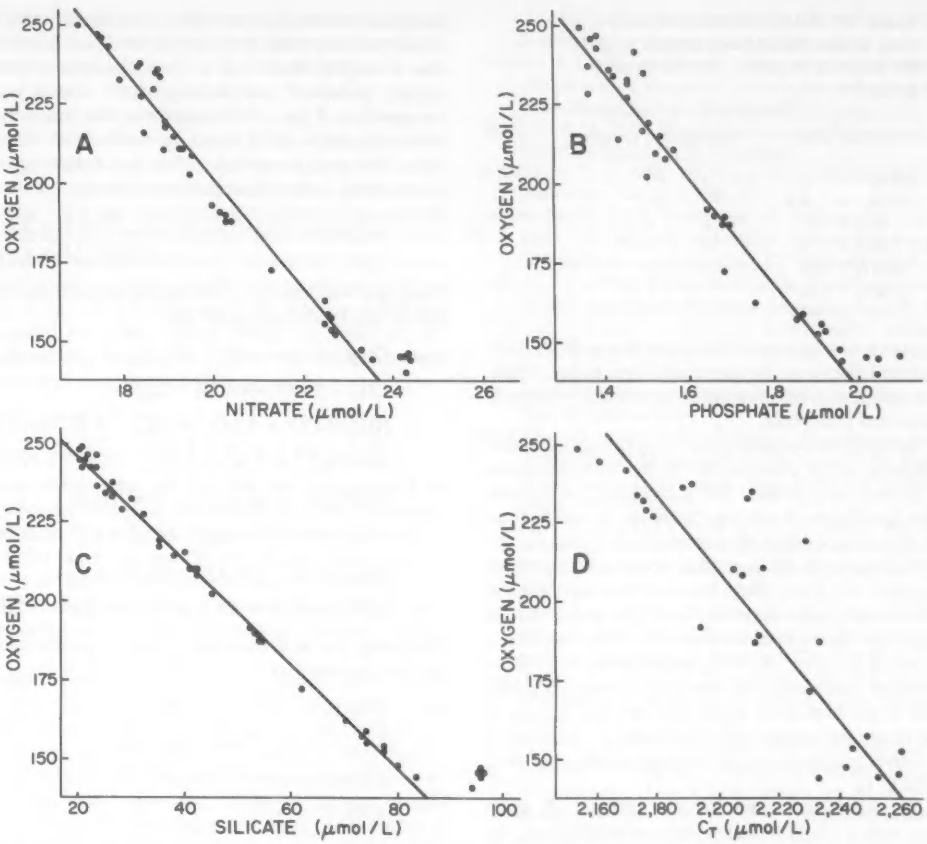

FIG. 2. Plots of oxygen versus regenerated nutrients and total inorganic carbon between 500 and 2300 m in Baffin Bay. Straight lines represent the least squares fit to data between 500 and 1800 m. C_T = total inorganic carbon.

Thus, for this part of the water column, while NO and PO as derived from eq. 1 are not conservative quantities, (NO)′ = 549 and (PO)′ = 470 are. The main implication of this result is that the Redfield–Ketchum–Richards model is not representative of decaying matter in Baffin Bay. In particular, the relative amount of nitrogen with respect to phosphorus is about 9.6 rather than 16, as the Redfield–Ketchum–Richards model predicts. While this result is a little surprising at first, it is consistent with our measurements of highly depleted nitrate near the surface above a strong pycnocline (essentially zero in the top 25 m of the water column) and with results of laboratory measurements of plankton grown in nutrient-limited environments that show N/P ratios as low as 5 (Eppley 1972; Goldman et al. 1979).

Preformed nutrients can in principle be used to trace the water masses that have entered Baffin Bay through Davis Strait and Smith Sound. The water in Baffin Bay is mostly colder and slightly fresher than Atlantic water that enters through Davis Strait (Coote and Jones 1982) or that is found near Svalbard, the nearest location to Baffin Bay for which extensive chemical data are available (Anderson and Dyrssen 1980, 1981). Under the assumption that processes that have caused these changes do not much affect the oxygen content or values of preformed nutrients, we can compare values for preformed nutrients in Baffin Bay with concentrations in Atlantic water at these two locations by using the values of oxygen found at these locations in eq. 3 and 4. The calculated values for $[NO_3^-]_{pre}$ are 13.5 μmol/L compared with 10.4 μmol/L for water near Svalbard at a depth of 200–500 m and 15.1 μmol/L compared with 16 μmol/L at Davis Strait. The calculated values for $[PO_4^{3-}]_{pre}$ are 1.0 μmol/L compared with 0.8 μmol/L near Svalbard and 1.1 μmol/L compared with 1.1 μmol/L at Davis Strait. The agreements between the calculated preformed values and measured values are better for Davis Strait than for Svalbard as one might expect given the relative proximity of the two locations with respect to Baffin Bay. Differences can arise because of effects produced in Baffin Bay during processes that modify salinity and temperature or, especially for water entering through Smith Sound, because of processes occurring on the way to Baffin Bay.

The silicate data between 500 and 1800 m also show a highly linear relationship with oxygen (Fig. 2C), which can be fit with the equation

(9) $[O_2] = -1.65[SiO_2] + 278$ ($r^2 = -0.997$).

This correlation is an unusual feature, since unlike nitrate (or phosphate), there is no a priori reason to expect silicate concentrations to be related to oxygen consumption. The high correlation between silicate and oxygen concentrations might mean that the silicate distribution is determined primarily by dissolution in the water column at a rate proportional to the rate

TABLE 1. Relative amounts of components of the modified stoichiometric model for decaying biogenic material in deep Baffin Bay.

Chemical shifts	Component values
$\Delta PO_4^{3-} = 1$	$s = 63$
$\Delta NO_3^- = 9.6$	$t = 46$
$\Delta C_T = 135$	$u = 8.7$
$\Delta A_T = 0$	$v = 0.87$
$\Delta SiO_2 = 102$	$x = 102$
$\Delta O_2 = 168$	$y = 5.7$

of oxygen consumption by organic nitrogen and carbon. Such an excellent correlation with oxygen consumption could indicate that most silicate regeneration occurs at locations similar to those for nitrate and phosphate.

Inorganic carbon produced during the decay of organic matter makes a relatively small contribution to the total inorganic carbon (C_T) present in seawater. Since inorganic carbon can come from the dissolution of calcium carbonate as well as from the oxidation of organic carbon, the correlation between C_T and oxygen will not, in general, be as good as between phosphate or nitrate and oxygen. In Baffin Bay, the data between 500 and 1800 m do show a correlation between C_T and oxygen, although not to the same high degree as do the nutrients. The slope for C_T vs oxygen is about 0.8 (Fig. 2D). The contribution to C_T from calcium carbonate dissolution as estimated from alkalinity measurements is no more than about one-half the change in alkalinity due to nitrate regeneration, too small to be observed given the relative precision of the measurements (see next section and Table 1).

In Baffin Bay Bottom water, below 1800 m, all three nutrients have values slightly higher than expected from the oxygen vs nutrient relationships for the water between 500 and 1800 m of North Atlantic origin. If Baffin Bay Bottom water also originates in the North Atlantic, these slightly higher nutrient values can be explained by some nutrient regeneration occurring in the sediments. Measurements of nitrate and phosphate in sediment porewater have not been made; however, silicate measurements in sediment porewater from samples collected from central Baffin Bay show a fairly pronounced increase with depth ($\approx 20\ \mu mol \cdot L^{-1} \cdot cm^{-1}$), indicating a silicate flux from the sediments. While not confirming the origin of Baffin Bay Bottom water, these results are consistent with a North Atlantic origin (Muench 1971) if there is a small nutrient flux from the sediments.

Stoichiometric Composition of Biogenic Material

We base our discussion on a modified version of the Redfield–Ketchum–Richards model, which includes the decay of both soft and hard parts of plankton (Dyrssen 1977; Anderson and Dyrssen 1981). Changes in total alkalinity (A_T), C_T, nitrate, phosphate, silicate, and oxygen are related to the oxidation and dissolution of biogenic material containing carbohydrate groups (CH_2O), lipid groups (CH_2), proteins or peptide groups ($NHCH_2CO$ and $NHCH_2CS$), phosphate ester groups ($CHPO_4M$), calcium carbonate ($CaCO_3$), and silica (SiO_2). Metal ions in the phosphate ester group are represented by M. A peptide link containing $-CH_2-CH(NH_2)-COO-$ might correspond better to the nitrogen content of planktonic proteins (Parsons et al. 1977), but to maintain a relatively simple model, the hydrocarbon groups are included in the lipid part with the $-CH_2-$ link in the model polymer. The phosphate ester link, $-CH(OPO_3M)-$, is also a simplification, but a more elaborate representation of organic phosphate will hardly affect relative values of the components of the stoichiometric model, since the amount of carbon bound to phosphorus is small. With these considerations, the model substance has the following composition (normalized to one phosphate ester group):

$$(CH_2O)_s(CH_2)_t(NHCH_2CO)_u(NHCH_2CS)_v \times (CHPO_4M)(SiO_2)_x(CaCO_3)_y.$$

The equations describing the oxidation and dissolution for each part of this model substance are

$$\begin{aligned}
&CH_2O + O_2 \rightarrow CO_2 + H_2O\\
&CH_2 + 1.5O_2 \rightarrow CO_2 + H_2O\\
&NHCH_2CO + 3.5O_2 \rightarrow NO_3^- + H^+ + 2CO_2 + H_2O\\
&NHCH_2CS + 5.5O_2 \rightarrow NO_3^- + 2H^+ + 2CO_2 + HSO_4^-\\
&CHPO_4M + O_2 \rightarrow CO_2 + MHPO_4\\
&CO_2 + MHPO_4 + H_2O \rightarrow CO_2 + M^{2+} + H_2PO_4^- + OH^-\\
&SiO_2(\text{solid}) + 2H_2O \rightarrow Si(OH)_4\\
&CaCO_3(\text{solid}) + CO_2 + H_2O \rightarrow Ca^{2+} + 2HCO_3^-.
\end{aligned}$$

The changes in total alkalinity, total inorganic carbon, nutrients, and oxygen are thus

$$\begin{aligned}
&\Delta A_T = 2y - 1 - u - 2v\\
&\Delta C_T = s + t + 2(u + v) + 1 + y\\
&\Delta NO_3^- = u + v\\
&\Delta PO_4^{3-} = 1\\
&\Delta SiO_2 = x\\
&\Delta O_2 = -(s + 1.5t + 3.5u + 5.5v + 1).
\end{aligned}\tag{10}$$

From the nutrient, carbon, and oxygen data we can obtain the values for the amount of each component of the modified stoichiometric model except the sulphur- and calcium-containing parts. Neither sulphate nor calcium was measured; however, we can estimate the change in calcium from the change in alkalinity (ΔA_T was approximately equal to 0). For sulphate, we assume $v = 0.1u$, a not atypical value for the relative amount of sulphur in proteins.

The results are presented in Table 1. Probably the most dramatic feature is the low N/P ratio already commented upon in the discussion of NO and PO. The total inorganic carbon measurements were not precise enough to give reliable estimates for s and t, the relative amounts of carbohydrate and lipid groups in the modified stoichiometric model, because these values are very sensitive to the value for ΔC_T. The uncertainty in ΔC_T is large enough to include values of s both greater and less than t, although the former is more reasonable than the latter, since diatoms (which are dominant in Baffin Bay) will have a low lipid to carbohydrate value.

Consequences for Fossil Fuel CO_2 in the Ocean

The modified stoichiometric model illustrates in more detail than does the Redfield–Ketchum–Richards model how overall relationships between carbon and oxygen can be affected during decay by changes in the relative amounts of the components of the model. While for biological studies small variations among these components may not be especially relevant, they could be crucial in assessing the amount of fossil fuel carbon dioxide that has entered the ocean. The contribution of fossil fuel carbon dioxide to C_T is small, not much above 1% (e.g. Broecker et al. 1979), and can be determined only if all other processes affecting C_T are taken into account. An important contribution to C_T is, of course, carbon from decaying biogenic material. In papers that deal with the observation of fossil fuel carbon dioxide in the ocean, this contribution has been determined from changes in oxygen concentrations using the Redfield–Ketchum–Richards model to relate carbon production to oxygen utilization, i.e. $\Delta C_T/\Delta O_2 = 0.768$ (Brewer 1978; Chen and Millero 1979; Jones and Levy 1981; Chen 1982). In terms of the modified stoichiometric model, the relationship between carbon production and oxygen utilization from eq. 10 is

$$(11)\quad \Delta C_T/\Delta O_2 = -[s + t + 2(u + v) + 1 + y] \div (s + 1.5t + 3.5u + 5.5v + 1).$$

From this relationship, one can see that the measurement of oxygen utilization to determine the contribution of carbon from biogenic decay to C_T will be affected by the nitrogen to phosphorus ratio, $u + v$, and by the relative amounts of carbohydrates and lipid components, s and t. Basically, the former occurs because phosphorus is not oxidized and the latter because each component requires different amounts of oxygen during decay.

As an example, we use our data from Baffin Bay, where $\Delta C_T/\Delta O_2 = 0.8$. Changing the nitrogen to phosphorus ratio from the observed value of 9.6 to the more usual value of 16 gives $\Delta C_T/\Delta O_2 = -0.77$, nearly 4% change, which corresponds to about 25% of the maximum reported contribution to C_T from fossil fuel carbon dioxide. While this change in the nitrogen to phosphorus ratio is relatively large, it is within a range observed in nature. Similarly, increasing s by 15%, but keeping $s + t$ the same, results in a comparable change in $\Delta C_T/\Delta O_2$. Few results seem to be available to determine the variations that could occur in s and t. One study (Smith and Morris 1980) found that in phytoplankton in the southern ocean the lipid fraction was 80% of the total amount of fixed carbon. Generally, much smaller but varying lipid fractions were observed in other locations and seasons, ranging to as low as 10%. Clearly, these variations would have considerable effect on the $\Delta C_T/\Delta O_2$ ratio if they were reflected in the composition of the biogenic material decaying in the water column. Thus, while the modified stoichiometric model is not a complete representation of decaying biogenic material, it does perhaps offer a more complete accounting of oxidative processes and could help provide a more accurate assessment of the amount of fossil fuel carbon dioxide that has entered the ocean.

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Interrenal, Thyroidal, and Carbohydrate Responses of Rainbow Trout (*Salmo gairdneri*) to Environmental Acidification

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Exposure to acid-treated water (H_2SO_4, pH 6.0–4.2) for 21 d altered interrenal and thyroid function in immature rainbow trout, *Salmo gairdneri*. At a pH < 5.2 plasma cortisol increased, implying sustained interrenal cortisol release. Interrenal histology showed hyperplasia and elevated nuclear diameter at pH 4.7. Eight days of acid exposure (pH 4.7) were required to raise plasma cortisol significantly. At a pH < 4.7 the ratio of plasma T_4 (L-thyroxine) to T_3 (3,5,3′-triiodo-L-thyronine) tended to increase in relation to the controls. Depending on the experiment, this was due to either a significant elevation in plasma T_4 or a decrease in plasma T_3. No histological changes were evident in the thyroid of acid-treated trout. Eight days of acid exposure (pH 4.7) were required to depress plasma T_3. Coincidental with higher interrenal activity, plasma glucose was elevated in acid-treated fish (pH < 5.2) after 4 d of exposure. The possible relationships of the endocrinde changes to accompanying acid-induced elevations in plasma glucose and protein and hepatocyte histochemistry are considered, and their possible roles as indices of acid stress are discussed.

L'exposition à de l'eau acidifiée (H_2SO_4, pH 6,0–4,2) pendant 21 jours a modifié les fonctions interrénale et thyroïdienne chez la truite arc-en-ciel (*Salmo gairdneri*) immature. À un pH 5,2, le niveau de cortisol plasmatique a augmenté, ce qui suppose la libération prolongée de cortisol interrénal. L'examen des préparations histologiques de tissus interrénaux a révélé une hyperplasie et des diamètres nucléaires élevés à un pH de 4,7. Il a fallu huit jours d'exposition à l'acide (pH 4,7) pour augmenter le niveau de cortisol plasmatique de façon significative. À un pH 4,7, le rapport entre les plasmas T_4 (L-thyroxine) et T_3 (3,5,3′-triiodo-L-thyronine) avait tendance à augmenter comparativement aux groupes témoins. Selon l'expérience, cela dépendait soit d'une augmentation prononcée du plasma T_4 ou d'une baisse du plasma T_3. Aucun changement au niveau histologique n'était évident dans la thyroïde des truites traitées à l'acide. Huit jours d'exposition à l'acide (pH 4,7) ont été nécessaires pour réduire le niveau du plasma T_3. Coïncidant avec une activité interrénale supérieure, le niveau de glucose plasmatique était élevé chez les poissons exposés à l'acide (pH $< 5,2$) pendant 4 jours. Le rapport présente les relations possibles entre, d'une part, les changements endocriniens par suite des augmentations du glucose et des protéines plasmatiques causées par l'acide et, d'autre part, l'histochimie des hépatocytes, et il montre aussi les rôles potentiels de ces relations en tant qu'indices du stress acidique.

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The physiological problems encountered by freshwater fish in acidic waters have been the subject of numerous recent investigations. Disturbances in acid–base balance and ionic–osmotic regulation have been implicated as key toxic mechanisms (McWilliams and Potts 1978; Neville 1979a, 1979b; Packer 1979; McWilliams 1980; Graham and Wood 1981; McDonald and Wood 1981; Booth et al. 1982). Limited research has been conducted on other physiological factors affected by acidification.

In addition to the specific physiological responses of an organism to a stressor, a series of nonspecific physiological responses, referred to as the general adaptation syndrome (GAS), takes place in mammalian vertebrates (Selye 1950). The stress response in teleostean fish is considered to be similar in nature to the GAS (Schreck 1981). Stressful stimuli rapidly activate the hypothalamo–pituitary–interrenal (HPI) and adrenergic systems, which mediate changes in carbohydrate and hydromineral balance (Mazeaud et al. 1977), but it remains to be demonstrated that chronic acid stress activates the HPI axis. In one of the few studies conducted, serum cortisol of rainbow trout, *Salmo gairdneri*, exposed to low pH (7.0–4.2) was shown not to differ from controls (Lee et al. 1983).

The effects of stress, in any form, on other endocrine systems of fish have received far less attention (Pickering 1981). However, there are indications that the thyroidal systems may respond to both acute and chronic stress (Osborn and Simpson 1974; Simpson 1976; Brown et al. 1978; Leatherland and Sonstegard 1978; Eales 1979). Because adequate thyroidal status seems to be required for normal growth and reproduction (Sage 1973; Eales 1979; Leatherland 1982; Higgs et al. 1982) and for maintenance of blood Na^+ concentration and osmotic balance (Knoeppel et al. 1982), acid precipitation could influence fish detrimentally by altering thyroid function.

Our objective has been to define changes in plasma cortisol and thyroid hormones during 21 d of acid treatment (pH range 4.2–6.0). This was supported by histological examination of interrenal and thyroid tissues. Also, plasma glucose levels were monitored because elevated blood glucose appears to be mediated, in part, by increases in plasma cortisol (Leach and Taylor 1980, 1982) and it is a frequently used indicator of stress. Further understanding of biochemical stress responses in fish exposed to acid and the degree to which they adapt could provide important biological indicators of acidification and are relevant when considering the limits of change to the environment that can be allowed.

Materials and Methods

Experimental Animals

Rainbow trout (weight, 198 ± 3 g; fork length, 25.3 ± 0.1 cm; $\bar{x} \pm$ SE, $N = 330$) were obtained from the Rockwood Hatchery, Freshwater Institute. Fish were held in 500-L fiberglass tanks with flowing, aerated, dechlorinated Winnipeg City water which contained the following major ion concentrations: 0.51 mmol $Ca^{2+} \cdot L^{-1}$, 0.24 mmol $Mg^{2+} \cdot L^{-1}$, 0.14 mmol $Cl^- \cdot L^{-1}$, 0.08 mmol $Na^+ \cdot L^{-1}$, and 0.04 mmol $K^+ \cdot L^{-1}$. Hardness was equivalent to 0.75 mmol $CaCO_3 \cdot L^{-1}$ (75.1 $mg \cdot L^{-1}$). The average pH of the water was 7.7 (95% confidence interval, 7.64–7.80). Dissolved inorganic carbon measured by gas chromatography (Stainton et al. 1974) was 1.43 ± 0.04 $mmol \cdot L^{-1}$ ($\bar{x} \pm$ SE).

Toxicity Testing

Fiberglass tanks (125 L) or glass aquaria (70 L) were used to expose the fish to H_2SO_4 in groups of 7–12 per tank. All tanks had translucent white Plexiglas tops and the sides of the aquaria were covered with black polyethylene. Each tank received at least 2 L of aerated water per gram of fish each day. Test water was obtained by an acidification–decarbonation system consisting of a Radiometer titrator (model TTT2 or TTT80) and a Bach–Simpson six-channel automatic switch. In addition, the pH of the test tanks was continuously monitored by a titrator or a titrator and a six-channel switch. Instrument calibrations were checked three times daily against a standardized Radiometer pH meter. Radiometer magnetic valves or Masterflex pumps with Radiometer magnetic relays were used to add acid. No metal components were in contact with the test water.

The CO_2 produced by acidification was removed via an air stripping procedure so that P_{CO_2} averaged 44.2 ± 2.2 $\mu mol \cdot L^{-1}$ ($\bar{x} \pm$ SE, $N = 20$) in the test tanks containing fish. Trout were acclimated to the test tanks for 10–14 d prior to testing. To avoid a large CO_2 surge at the onset of each experiment, acidified water (pH 5.0), stripped of excess CO_2 and up-titrated to pH 7.7 with NaOH, was supplied to each test tank for a time equivalent to 99% replacement of the water volume. Then the tank was acidified to its nominal pH. The entire process was complete in 6–8 h. During this time the P_{CO_2} was monitored at 60-min intervals. As the water in the tank was replaced with up-titrated, stripped water the mean P_{CO_2} decreased from 57 to 19 $\mu mol \cdot L^{-1}$ ($N = 20$). When the water was reacidified the average P_{CO_2} increased to 44 $\mu mol \cdot L^{-1}$ and remained stable throughout the experiments.

The water temperature ranged seasonally from 11.5 to 14.1°C but during any one experiment varied less than 1°. The photoperiod was adjusted to 14 h of light and 10 h of darkness. Fish were fed Martin Feeds trout food (Elmira, Ontario) at an amount equaling 1% wet body weight every second day. The fish from each tank were starved for 4 d prior to each sampling.

The effects of acid on trout were investigated in three experiments. In Exp. 1, fish were exposed to five different pH levels (7.7, 6.0, 5.2, 4.7, and 4.2) for 21 d prior to sampling. The experiment was repeated and the combined results are presented. The time-course of the response was examined in Exp. 2 at pH 4.7 and Exp. 3 at pH 5.2 with sampling at 1, 2, 4, 8, 16, and 21 d of exposure. For Exp. 1 and 2, trout from a control tank (pH 7.7) and a tank containing acidified water that was up-titrated with NaOH (pH 7.7) were sampled. No difference could be found for any parameter examined and data are not given.

Blood Sampling and Analysis

To avoid possible netting and sampling effects on cortisol (Pickering et al. 1982), trout were anaesthetized directly in the test tanks with tricaine methanesulphonate (TMS, 0.2 $g \cdot L^{-1}$), neutralized to tank pH with NH_4OH (Barton et al. 1980). Immobilization was complete within 30 s. Blood was removed from the caudal vessels within 1–2 min using preheparinized 3- or 5-mL syringes and 18-gauge needles. Plasma was immediately separated by centrifugation and stored at −20°C in polyethylene vials. To minimize potential diurnal effects, samples were taken between 13:00 and 15:00 each day and usually analyzed within 10 d.

Radioimmunoassays for T_4 (L-thyroxine) and T_3 (3,5,3′-triiodo-L-thyronine) were by the procedures of Brown and Eales (1977). Cortisol radioimmunoassay was done with commercially available kits (Micromedic Systems, Inc., Horsham, PA). Although there was parallelism between cortisol standards and dilutions of trout plasma to 5 $ng \cdot L^{-1}$, lower dilution diverged from the standard curve. In addition, the bound fraction from several trout samples contained greater ^{125}I-labeled cortisol counts than the 0 level standard. This was corrected by preparing standards with rainbow trout plasma that had the endogenous steroids removed by incubation with charcoal (Mitsuma et al. 1972; Abraham et al. 1977). The assay protocol used 20 μL of a 1:10 dilution of plasma for measurement. This volume could be increased to 100 μL, giving a fivefold increase in sensitivity without altering other assay characteristics. Furthermore, assays were more reproducible and sensitive if the antibody equilibrium step was carried out at 4°C for 16 h. The coefficient of reactivity at 50% displacement (CR50%) of labeled cortisol was determined for each of 14 steroids (Abraham 1975). Steroids giving greater than 0.1 CR50% with the cortisol antibody were prednisolone (31.0), 11-deoxycortisol (28.0), 11-deoxy-7-hydroxycorticosterone (22.0), 17-hydroxyprogesterone (4.6), cortisone (0.8), prednisone (0.6), corticosterone (0.2), and 17-hydroxypregnenolone (0.1). Intra-

TABLE 1. Effects of pH (95% confidence interval) on mortality, plasma cortisol, glucose, protein, T_4, T_3, T_4:T_3, and interrenal nuclear diameter in rainbow trout exposed for 21 d. Values represent mean (±SE) of 9–18 fish. *Significantly different from pH 7.6–7.8 ($P < 0.05$).

pH interval	Mortality (%)	Cortisol ($ng \cdot mL^{-1}$)	Glucose ($mg \cdot mL^{-1}$)	Protein ($mg \cdot mL^{-1}$)	T_4 ($ng \cdot mL^{-1}$)	T_3 ($ng \cdot mL^{-1}$)	T_4:T_3	Interrenal nuclear diameter (μm)
4.19–4.23	50.0	82.5* (20.5)	2.43* (0.49)	32.7* (3.3)	1.94* (0.46)	1.01 (0.19)	2.38* (0.67)	6.05* (0.11)
4.65–4.74	33.3	60.9* (22.7)	2.18* (0.46)	29.0* (2.6)	1.34 (0.28)	1.15 (0.15)	1.58* (0.40)	5.67 (0.10)
5.17–5.25	11.1	7.5* (3.1)	1.65* (0.41)	26.7 (2.8)	0.64 (0.10)	1.39 (0.23)	0.62 (0.11)	5.47 (0.08)
5.98–6.04	0.0	2.9 (1.7)	0.85 (0.04)	24.8 (1.6)	0.67 (0.11)	1.16 (0.21)	0.75 (0.15)	5.44 (0.11)
7.64–7.84	0.0	1.3 (3.3)	0.72 (0.04)	25.4 (1.9)	1.12 (0.19)	1.51 (0.21)	0.94 (0.17)	5.49 (0.12)

assay coefficient of variation (CV) from 10 duplicate analyses of the same sample was 5.4%. Intraassay CV of duplicate analyses from 10 assays was 9.1%. Recoveries of cortisol (1–50 $ng \cdot mL^{-1}$) added to rainbow trout plasma ranged from 93.5 to 112.0%. The minimum level of sensitivity, defined as the dose level 2 standard deviations away from the 0 dose measurement, averaged 1 $ng \cdot mL^{-1}$ over 10 assays.

Plasma glucose concentrations were determined employing a Sigma test kit (No. 510), which is based on use of glucose oxidase and peroxidase with *o*-dianisidine as chromagen. The interassay CV equaled 5.9% from 10 duplicate measurements on the same sample, and interassay CV in duplicate analyses from 10 assays was 7.9%. Minimum detectable level of glucose was 0.17 $mg \cdot mL^{-1}$ and recovery of added glucose (0.25–1.0 $mg \cdot mL^{-1}$) ranged from 92 to 96%. Plasma protein was determined according to the method of Lowry et al. (1951) using crystalline bovine serum albumin as standard. Intraassay and interassay CV were 7.1 and 8.4%, respectively.

Histopathology

The head kidneys (interrenals) and portions of the first four gill arches (thyroid) were removed from each fish and fixed in Bouin's solution. After washing for 2 d in 70% ethanol, the head kidneys were embedded in paraffin. Prior to embedding, thyroid tissues were decalcified for 3 d in 70% ethanol containing 3% HCl and then washed for 24 h in 70% ethanol. Tissue sections were cut at 10 μm and stained with Harris' hematoxylin and eosin (Edwards 1967). To determine interrenal nuclear size, 50 round nuclear diameters for each fish were measured with an ocular micrometer. Because trout interrenals are diffusely distributed cords or clusters of cells, measurements were made from three different areas of the head kidney.

Interrenal Δ^5-3β-hydroxysteroid dehydrogenase (Δ^5-3β-HSDH) activity was determined by the histochemical method of Wattenberg (1958). Fresh, frozen, cryostat sections (15 μm) of head kidney from control and pH 4.7 exposed fish (21 d) were used. The substrates were dehydroepiandrosterone and 5-pregnenolone, the former producing a better response. Sections were incubated for up to 2 h at 37°C.

For glycogen and cellular changes, small pieces of liver from controls and fish exposed to pH 4.7 (4–22 d) were fixed for 24 h in phosphate-buffered (pH 7.2) glutaraldehyde (2.5%), post-fixed in 1% phosphate buffered osmium tetroxide (1 h), and embedded in Epon. Tissue sections of 1 μm were stained with 1% toluidine blue in 1% aqueous borax, and for glycogen with the PAS method of Lane and Europa (1965).

Data Analysis

Differences in given parameters between groups of fish and experiments were tested by one-way or two-way analysis of variance. Where appropriate, Duncan's multiple range test was used to distinguish differences between means from more than two groups of fish. A probability level of <0.05 was considered significant. Bartlett's test was applied to insure homogeneity of variance and in some cases data were log transformed to obtain uniform variance. However, for clarity of presentation, arithmetic means with standard errors have been used in tables and figures. The Pearson product moment correlation was used to test the relationships between cortisol, T_4, T_3, glucose, and interrenal responses to different pH or times of exposure to a pH.

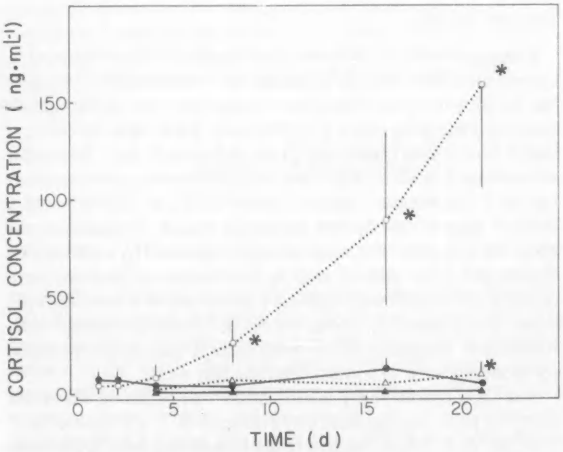


FIG. 1. Temporal changes of plasma cortisol concentrations in trout exposed to pH 4.7 (○) and pH 5.2 (△). Control fish at pH 7.7 (●, ▲) were examined at each time. Points represent mean ± SE of 7–12 fish. Means significantly different from control are indicated with an asterisk.

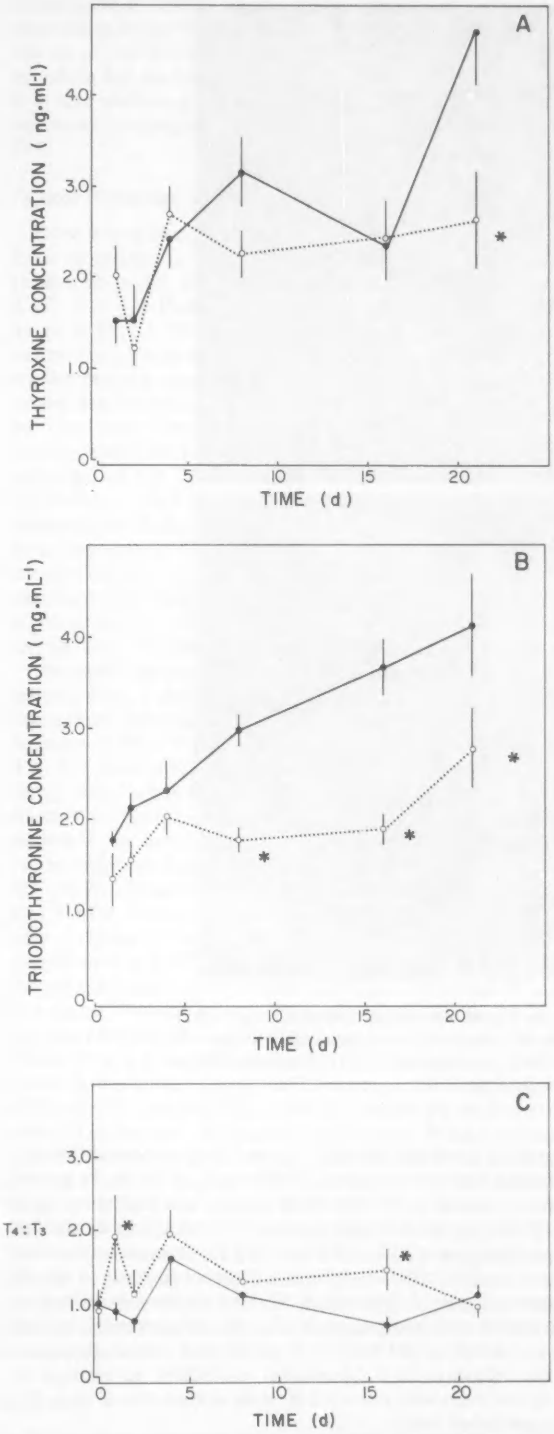


FIG. 2. Temporal changes of (A) plasma thyroxine and (B) triiodothyronine concentrations and (C) their ratios in trout exposed to pH 4.7 (○) and pH 7.7 (●). Points represent mean ± SE of 10–12 fish. Means significantly different from control are indicated with an asterisk.

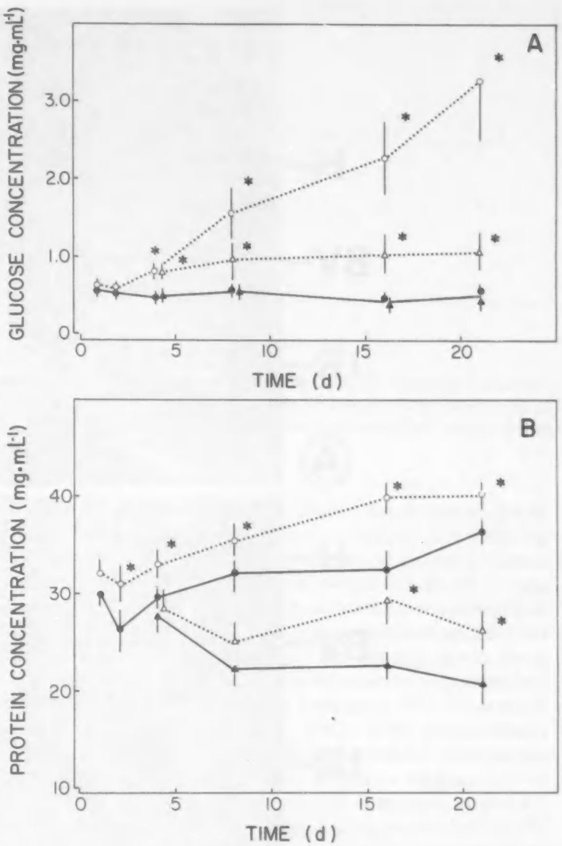


FIG. 3. Temporal changes of (A) plasma glucose and (B) plasma protein in trout exposed to pH 4.7 (○) and pH 5.2 (△). Control fish at pH 7.7 (●, ▲) were examined at each time. Points represent mean ± SE of 7–12 fish. Means significantly different from control are indicated with an asterisk.

Results and Discussion

Mortality

Loss of equilibrium and deaths began after 7 d of exposure to pH 4.2 and after 18 d of exposure to pH 4.7 or 5.2. Survival of 50% of the fish at pH 4.2 (Table 1) in moderately hard water corresponds to LC50 values for 21 d of exposure of similar sized trout (M. Giles, Freshwater Institute, Winnipeg, Man., personal communication). No mortalities occurred in trout held at pH 6.0 or 7.7. The most notable behavioral alteration in fish held at pH 4.2 or 4.7 was their reluctance to feed after 7–10 d.

Cortisol

Plasma cortisol in undisturbed control fish was generally less than 5 ng·mL^{-1}, a result in agreement with those of McBride et al. (1975, 1979), Barton et al. (1980), Swift (1981a, 1981b, 1982), and Barton and Peter (1982). This value was lower than reported from some earlier studies (Hill and Fromm 1968; Grant and Mehrle 1973; Sivarajah et al. 1978) and for brook trout, *Salvelinus fontinalis* (Mudge et al. 1977).

When trout were exposed to different pH levels for 21 d,

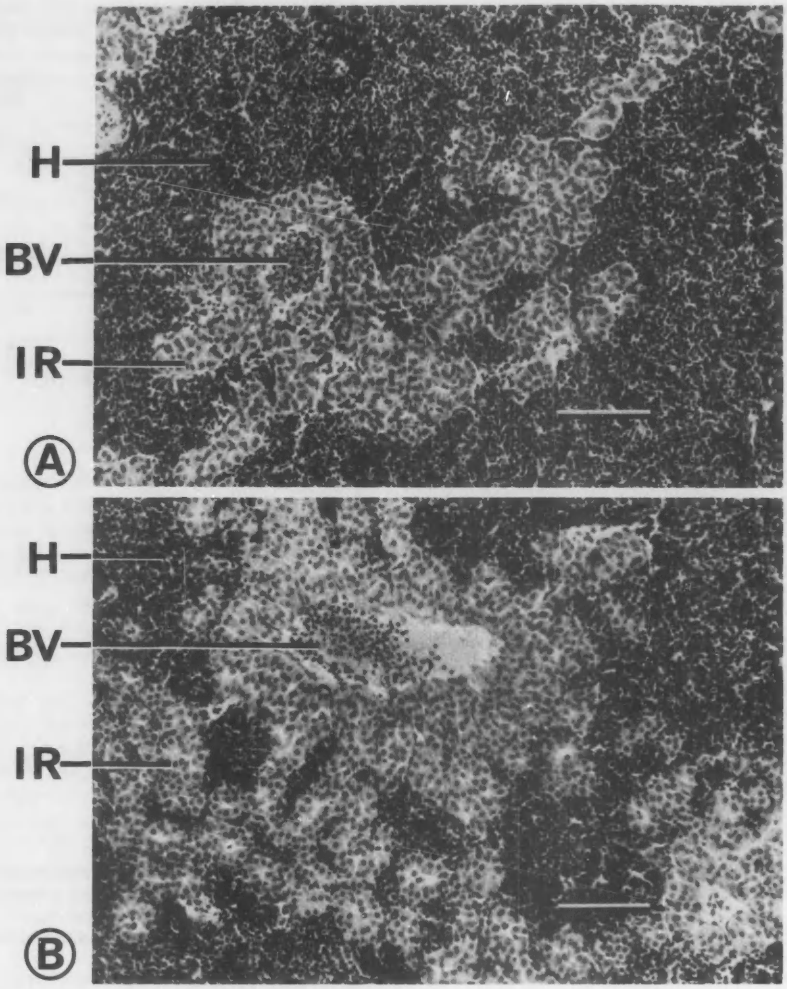


FIG. 4. Paraffin sections (10 μm) of trout head kidneys stained with Harris' hematoxylin and eosin. (A) Interrenal tissue (IR) in a control fish occurring in small lumps and cords irregularly distributed in the hemopoietic tissue (H), surrounding blood vessels (BV), or as discrete islets; (B) hyperplastic interrenal tissue after 21 d of exposure to acid (pH 4.7). Bar = 40 μm.

cortisol levels increased in a dose-dependent fashion (Table 1). The threshold occurred between pH 5.2 and 6.0. At pH 4.7, cortisol concentrations became significantly higher at 8 d and continued to rise over the course of the experiment (21 d) until death (Fig. 1). When trout were exposed to pH 5.2, blood cortisol levels were significantly elevated over control values only after 21 d. The magnitude of the response was approximately 10% that found in trout at pH 4.7. In contrast, plasma cortisol in acid-stressed rainbow trout (14–21 d, pH 7.0–4.2) from a previous study (Lee et a. 1983) did not differ significantly from controls. Also, Lockhart and Lutz (1977) found no difference between circulating cortisol levels in white sucker, *Catastomus commersoni*, captured from acidified (pH 4.8–5.3) George Lake and those captured from a nonacidified control area. However, it must be recognized that long-term adaptation or selection may occur in natural populations. Blood cortisol levels in brook trout acutely exposed (3–24 h) to acid (pH 4.0) showed transitory increases (Mudge et al. 1977). In the present study, cortisol may have been acutely elevated upon initial exposure to the acid and returned to basal values by the first sampling time at 24 h. The possibility that starvation stress may have contributed to the differential cortisol response to low pH seems unlikely. Milne et al. (1979) did not observe differences in plasma cortisol levels even after 65 d of starvation. In addition, cannulated fish have been examined in our laboratory and after recovery from cannulation procedures no changes in cortisol levels were observed in rainbow trout starved up to 21 d (unpublished data).

Use of a physiological stress response such as plasma cortisol is limited in that the response is generalized for many stressors (Thomas et al. 1981). However, cortisol measurements may provide a useful indicator of the general well-being of fish

(Tomasso et al. 1981); usually, high cortisol levels have been observed in dying fish (Fagerlund 1967; Strange et al. 1977). The use of cortisol measurements may be particularly appropriate where fish are exposed to two or more sublethal stressors (e.g. acid and heavy metals or elevated CO_2), as the response represents the integrated effect of the components (Donaldson 1981).

Thyroid Hormones

Three weeks of exposure to pH 4.2 and 4.7 elevated plasma T_4 levels and the T_4:T_3 ratio (Table 1). Plasma T_4 levels (Exp. 1) were positively correlated with plasma cortisol levels (r = 0.467, N = 47). Plasma T_3 levels were not significantly altered by pH in Exp. 1. The pH 4.7 time exposure (Exp. 2) showed contrasting findings with Exp. 1, because acid-exposed trout did not demonstrate significant changes in plasma T_4 (Fig. 2A), control fish had increased T_4 levels at 21 d, and T_4 levels were not correlated with cortisol levels. Plasma T_3 levels rose steadily, from 1.72 to 4.14 $ng \cdot mL^{-1}$ in pH 7.7 (Fig. 2B), while acid-exposed fish failed to show such an increase and had significantly lower T_3 levels that did not rise until 21 d of exposure. No changes were evident for either plasma T_4 or T_3 or their ratios in the pH 5.2 exposure (Exp. 3, data not shown). For all experiments, plasma T_4 and T_3 levels were positively correlated with plasma protein concentrations in both acid-exposed (T_4, r = 0.441, N = 152; T_3, r = 0.260, N = 151) and control (T_4, r = 0.584, N = 124; T_3, r = 0.486, N = 124) trout.

The reason for the differences in plasma thyroid hormones between Exp. 1 and 2 was not clear but may be related to a seasonal or maturational effect. However, similar to Exp. 1, exposure to pH 4.7 (Exp. 2) tended to increase the T_4:T_3 ratio (Fig. 2C). Since no changes in thyroid histology (see Histopathology) were noted it is possible that the acid effects were directed primarily at the peripheral metabolism of thyroid hormones. An increase in T_4:T_3 could result from reduced T_4 to T_3 conversion, as described in starvation stress (Higgs and Eales 1977, 1978). Because experimental fish ate less than control fish after 7–10 d of acid exposure, it is possible that reduced food ratio contributed to the increase in T_4:T_3. An additional complication is that T_4 and T_3 exist in trout blood in both free and protein-bound forms (Falkner and Eales 1973) and during acid stress, plasma protein increases. Increases in plasma protein(s) responsible for binding T_4 and/or T_3 would tend to elevate plasma levels of T_4 and/or T_3. The difference in plasma protein levels between Exp. 1 and 2 may have contributed to the differential T_4 response. This could also explain the tendency of plasma T_4 to increase in acid stress, the reverse of the response reported for other chronic stress conditions where suppression of thyroid activity has been observed (Sage 1971; Osborn and Simpson 1972, 1974; Lewis and Dodd 1976; Pickering 1976; Simpson 1976; Leatherland and Sonstegard 1978; Eales 1979). However, increases in plasma protein levels cannot explain why plasma T_3 was depressed in both Exp. 1 and 2 relative to controls. Further work on the peripheral metabolism and protein binding of thyroid hormones is required to define acid effects on the trout thyroid.

Glucose

Blood glucose concentration is a frequently used indicator of stress in teleost fish (Wedemeyer and McLeay 1981), responding to a variety of stressors including pollutants (Silbergeld 1974; Hattingh 1976; McLeay 1977; Wedemeyer and Yasutake 1977; Thomas et al. 1980, 1981). Glucose levels increased with increasing H^+ concentration in Exp. 1 (Table 1). The threshold was between pH 5.2 and 6.0. Significant elevations in plasma glucose were detected after 4 d of exposure to both pH 4.7 and 5.2 (Fig. 3A). At pH 4.7, glucose continued to rise throughout the experiment, while at pH 5.2, glucose increased until 8 d and then remained constant. In fish, the hyperglycemic stress response is apparently mediated by increases in plasma cortisol and catecholamines (Nakano and Tomlinson 1967; Mazeaud et al. 1977; Leach and Taylor 1980, 1982). In the present study, plasma glucose levels were positively correlated with plasma cortisol in acid-exposed fish from all three experiments (r = 0.485, N = 150). Furthermore, in the assessment of chronic acid stress on rainbow trout, plasma glucose may be more useful as an indicator than plasma cortisol. Significant and sustained elevations of glucose were evident after 4 d of exposure to pH 5.2, while elevation of circulating cortisol was not evident until 21 d. Cortisol could still be at least partially responsible for the hyperglycemia because plasma hormone measurements at a given time do not necessarily reflect the rate of utilization. Recent studies in unfed rainbow trout (Lee et a. 1983) and a whitefish, *Coregonus peled*, and brown trout, *Salmo trutta fario* (Nieminen et al. 1982), exposed to acidic conditions also showed that pH can increase plasma glucose levels. In addition to providing a ready energy source during acid stress, elevations in plasma glucose may be important in maintaining plasma osmolality in view of declining blood ion levels (Bergstrom 1971; Bashamohideen and Parvatheswararao 1972; M. Giles, personal communication).

Overall, our findings support the contention that the blood sugar assay represents a good indicator of stress (Silbergeld 1974; McLeay 1977). Other studies show that plasma glucose response is dependent on strain, nutritional status, and temperature (Nakano and Tomlinson 1967; Chavin and Young 1970; Wendt and Saunders 1973; Wydoski et al. 1976; Wedemeyer and McLeay 1981). Further study involving these factors and acid stress may prove useful in determining the general applicability of the blood sugar assay to acid stress.

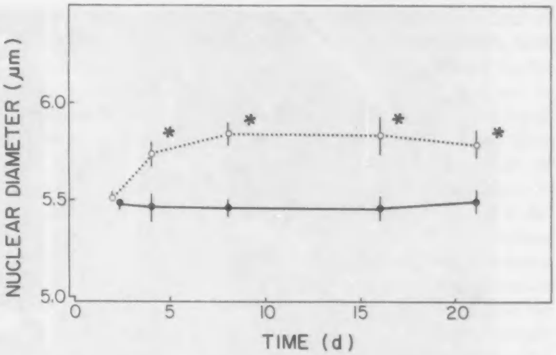


FIG. 5. Temporal changes of interrenal nuclear diameter in trout exposed to pH 4.7 (○) and pH 7.7 (●). Points represent mean ± SE of 7–10 fish. Means significantly different from control are indicated with an asterisk.

Protein

Plasma protein values were generally greater in trout exposed to H^+ than control fish (Table 1). The effect was significant at

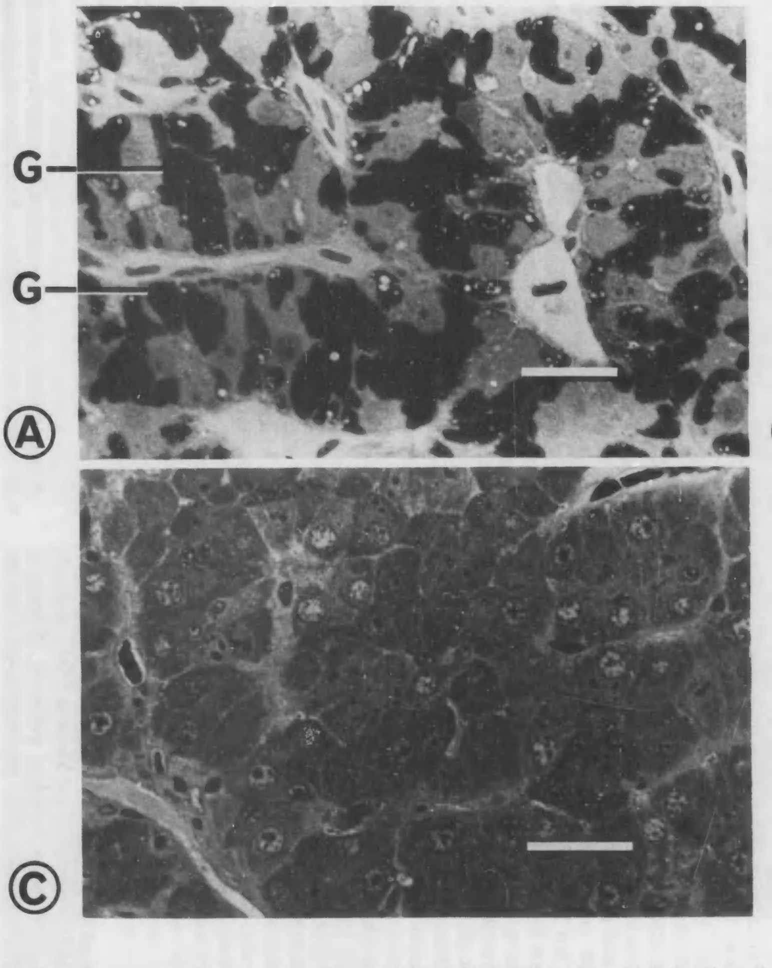
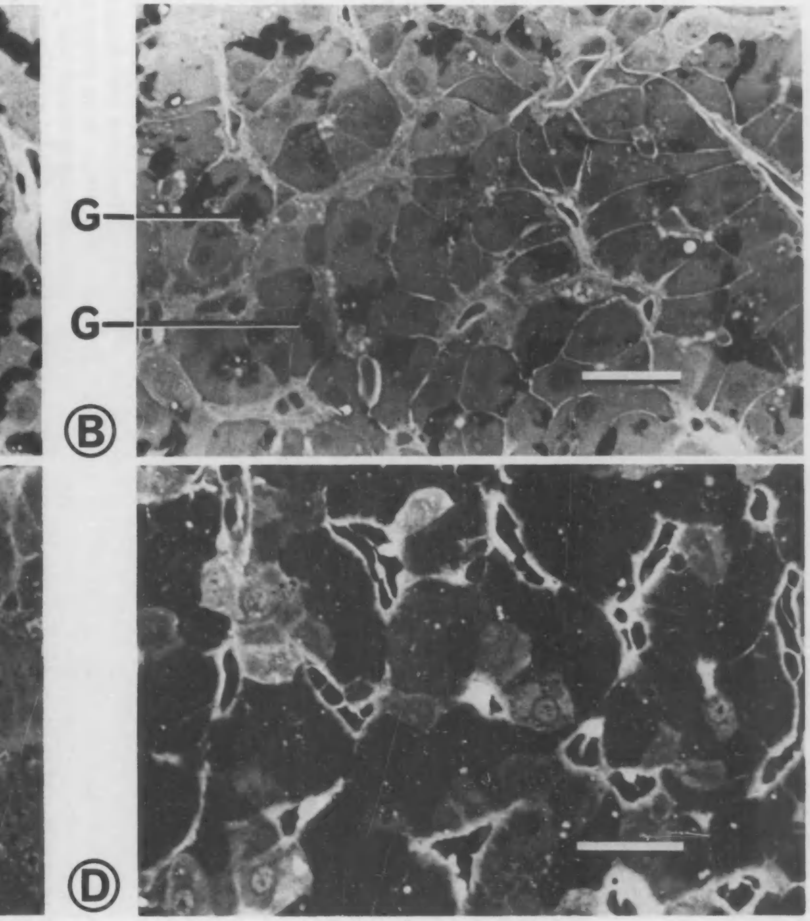


FIG. 6. Epon sections (1 µm) of trout liver. (A) Control (pH 7.7) stained with PAS to show gly
stained with toluidine blue to show clear nuclei and light cytoplasmic basophilia; (D) fish after 21 d
basophilia. Bar = 25 µm.



show glycogen (G); (B) fish after 21 d of acid exposure (pH 4.7) stained with PAS; (C) control (pH 7.7) fter 21 d of acid exposure (pH 4.7) stained with toluidine blue showing increased nuclear and cytoplasmic

pH 4.2 and 4.7 after 21 d. In Exp. 2, the elevation was apparent at 2, 4, 16, and 21 d but not at 8 d (Fig. 3B). In pH 5.2 water, higher plasma protein levels were found at 16 and 21 d (Fig. 3B). The cause for the increase is likely related to plasma volume changes associated with acid stress (Spry et al. 1981). Milligan and Wood (1982) found that 3 d of acid exposure (pH 4.0–4.5) reduced the plasma volume by 27% and increased protein by 90% in rainbow trout. Lockhart and Lutz (1977) found no effect of acidic (pH 4.8–5.3) George Lake waters on plasma protein of white suckers. As with plasma cortisol, long-term adaptation or selection may occur in natural populations. The increase in plasma protein (25%), in the present study, is not of sufficient magnitude to explain the 20- to 50-fold increase in plasma glucose and cortisol levels.

Histopathology

Previous investigations of interrenal activity in brook trout acutely exposed to acid (pH 4.0) showed histochemical evidence of decreased interrenal steroidogenesis (Mudge et al. 1977). In the present study more chronic exposure of rainbow trout below pH 5.0 clearly activates the HPI axis. There is interrenal hyperplasia and increased mitotic activity in trout at pH <4.7 (Fig. 4). Nuclear hypertrophy occurred at pH <4.7 (Table 1; Fig. 5). The enzyme, Δ^5-3β-HSDH, is important in the synthesis of most biologically active steroids from Δ^5-3β-hydroxysteroids (Wiebe 1969). The histochemical localization of Δ^5-3β-HSDH is a definite indication of potential steroid synthesizing capability of the interrenal cells (Watson and McKeown 1976). Following 21 d of acid exposure (pH 4.7) the enzyme's synthesizing potential appeared unchanged (data not shown). Contribution to higher circulating steroid levels likely arise from an increase in interrenal cell number. Elevated volumes of interrenal tissue have been previously observed in stressed rainbow trout (Robertson and Wexler 1959; McBride et al. 1975) and in other species (Oguri 1960; Hane et al. 1966; Erickson 1967).

Thyroid histology was not altered by exposure to acid (pH 4.7 or 4.2) for 21 d (data not shown). The follicles were oval or spherical and were not observed without colloid. Nuclei were centrally located in the squamous to cuboidal epithelial cells and nucleoli were prominent. Mitotic activity was not abundant.

Trout hepatocyte cytoplasm stained irregularly with toluidine blue, alternating light and dark regions being located variably in the cell. The dark regions represent areas of rough-surfaced endoplasmic reticulum. In control fish, hepatocyte nuclei and cytoplasmic basophilia were very light. The cytoplasm had dark blue lysosomes, moderate vacuolation, and few lipid droplets. The nuclei were generally easily observable with sharp outlines (Fig. 6). Following PAS staining, glycogen deposits appeared dense and occupied a major portion of the cells (Fig. 6). After 4 d of exposure to pH 4.7, cell basophilia increased. Following 21 d of exposure, cytoplasmic and nuclear basophilia was such that nuclei were difficult to discern. Basphilia is generally indicative of metabolically active cells. Our observations imply that trout hepatocytes become metabolically more active soon after acid exposure and maintain this adaptive condition throughout the experiment. Cell vacuolation and lipid deposits were similar to those of control liver; parenchymal cells and lysosomes were not as plentiful. Glycogen deposits were moderate to light after 4 d of exposure to acid (pH 4.7) and throughout the duration of the experiment (Fig. 6).

While acute stress depletes liver glycogen reserves (Morata et al. 1982), elevated liver glycogen can be a chronic effect of stress (Narasimhan and Sundararaj 1971) and treatment with adrenocorticosteroids (Chan and Woo 1978; Leach and Taylor 1982). Krishna-Murthy et al. (1981) noted a similar pattern in acid-exposed (pH 4.0) tilapia, *Tilapia mossambica*; after 1 d of exposure, liver glycogen reserves were reduced, while after 14 d, elevated liver glycogen was attributed to the onset of gluconeogenesis. Lee et al. (1983) showed similar increases in liver glycogen of rainbow trout exposed to low pH (4.8, 4.2) for 14 d. The apparent reduced glycogen reserves in trout under our experimental conditions may be associated with the reluctance of fish exposed to pH 4.7 or 4.2 to feed. Because starvation drastically reduced glycogen in the liver of rainbow trout (Milne et al. 1979), control fish feeding regularly would maintain higher liver glycogen levels. In contrast, rainbow trout used by Lee et al. (1983) were starved throughout the experiment. Starved fish at the higher pH levels (8.3–6.2) would have low liver glycogen reserves, and exposure to more acidic conditions (pH 4.8 or 4.2) may have resulted in a relative increase. Liver glycogen levels may be too dependent on nutritional state to provide a consistent indicator of acid stress.

Acknowledgments

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Planktonic Communities in Florida Softwater Lakes of Varying pH

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Brezonik, P. L., T. L. Crisman, and R. L. Schulze. 1984. Planktonic communities in Florida softwater lakes of varying pH. Can. J. Fish. Aquat. Sci. 41: 46–56.

In 20 softwater Florida lakes (pH range 4.7–6.8), phytoplankton diversity was significantly higher in the less acidic lakes; mean numbers of species in two groups (1, $\text{pH} < 5.3$; 2, $\text{pH} > 5.6$), each consisting of 10 lakes, was 10.8 and 16.5, respectively. Blue-green algae were dominant in less acidic lakes, while green algae were the most common group in acidic lakes. Phytoplankton abundance also was lower in acidic lakes, but covariation of phosphorus concentrations with pH confounded interpretation. Trends in zooplankton communities along the pH gradient were less pronounced. More acidic lakes had more species than the less acidic lakes, but three measures of species diversity showed no significant differences between the two groups. Zooplankton abundance was lower in the acidic lakes, but the relationship between abundance and pH showed much scatter. Lake productivity probably affects zooplankton abundance more than pH does in the sample group. No clear trends were observed in relative abundance of major zooplankton groups across the pH gradient. Six acid-tolerant species (including *Diaptomus floridanus*, *Eubosmina tubicen*, and *Daphnia ambigua*) were dominant in all 20 lakes.

Dans 20 lacs d'eau douce (où le pH varie de 4,7 à 6,8) de la Floride, la diversité du phytoplancton était sensiblement plus élevée dans les lacs les moins acides. Le nombre moyen d'espèces réparties en deux groupes (1, pH 5,3; 2, pH 5,6), chacun comprenant 10 lacs, s'élevait respectivement à 10,8 et à 16,5. Les algues bleues-vertes dominaient dans les lacs moins acides tandis que les algues vertes étaient les plus communes dans les lacs acides. L'abondance du phytoplancton était en outre moins élevée dans ces derniers mais la covariation des concentrations de phosphore avec le pH a brouillé l'interprétation. Les tendances des communautés de zooplancton par rapport au gradient du pH étaient moins prononcées. Les lacs plus acides contenaient davantage d'espèces que les moins acides, mais trois quantifications de la diversité des espèces n'ont pas révélé de différences significatives entre les deux groupes. La quantité de zooplancton était moins élevée dans les lacs acides mais la relation entre l'abondance et le pH a révélé une grande dispersion. La productivité lacustre influe probablement plus sur l'abondance du zooplancton que le pH dans les lacs échantillonnés. Aucune tendance précise n'a été observée pour ce qui est de l'abondance relative des principaux groupes de zooplancton par rapport au gradient du pH. Six espèces tolérantes par rapport aux conditions acides (y compris *Diaptomus floridanus*, *Eubosmina tubicen* et *Daphnia ambigua*) étaient en nombre dominant dans les 20 lacs.

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Acid precipitation is a well-documented phenomenon in northeastern North America, and numerous studies have been undertaken to evaluate its effects on aquatic ecosystems of that region (see Haines 1981; Cowling 1982). The effects of increased acidity on the composition of planktonic and fish communities are fairly well understood for temperate lakes, but many questions remain concerning the effects of acidification on biological processes such as primary production and mineral cycling.

Acid rain is not limited to northeastern North America. In the United States, the entire area east of the Mississippi River receives acid loadings from the atmosphere (e.g. see Likens et al. 1979; Cowling 1982), and other areas also are affected. Extensive studies in Florida (Brezonik et al. 1980, 1983) have shown that the northern two-thirds of the state receives bulk precipitation with an annual average $\text{pH} < 4.7$; data from wet/dry collectors indicate that rainfall pH throughout the state is 0.2–0.6 units lower than bulk precipitation pH. Excess (nonmarine) sulfate loadings in northern Florida amount to $7\text{–}11\ \text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, or roughly 50–80% of the loadings in the northeastern United States.

Acid precipitation is of particular concern in northern and central Florida because highly sandy soils are common throughout the region's interior uplands. The soils have low cation exchange capacities and low base saturation ratios. Similarly, many small lakes in upland sandhill areas have very soft waters and correspondingly low alkalinities. These lakes are sensitive to acidification from atmospheric loadings, as recent maps have illustrated (Omernik and Powers 1982). The effects of pH on community structure and ecosystem processes in warm temperate and subtropical lakes such as those in Florida are not well understood. No previous studies have evaluated trends in planktonic abundance and composition of Florida lakes over the pH range associated with acid precipitation.

As part of a broad effort to evaluate the significance of acid precipitation in Florida (Brezonik et al. 1983), we undertook a cross-sectional analysis of chemical and biological conditions along a pH gradient in softwater sandhill lakes. Description of variations in chemical conditions and nutrient status relative to pH and analysis of the sensitivity of the lakes to acidification is presented elsewhere (Hendry 1983; Hendry and Brezonik 1984). This paper describes the abundance and species composition of phytoplankton and zooplankton communities in the lakes in relation to pH.

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Methods

Two groups of softwater lakes were selected for the study: a group of 13 lakes in the Trail Ridge physiographic region of northcentral Florida (Alachua, Clay, and Putnam counties, 29°40′N, 82°00′W) and a group of 7 lakes in the Highlands Ridge physiographic region in southcentral Florida (Highlands County, 27°21′N, 81°20′W) (see Fig. 6-1 in Brezonik et al. 1983). The lakes range in pH from about 4.7 to 6.8, but they are otherwise similar in water chemistry. None of the lakes is eutrophic. Selection was based primarily on two criteria: soft water, making them sensitive to atmospheric loadings of acidity, and availability of data to determine whether pH and/or alkalinity had changed over the past 10–20 yr. Detailed descriptions of the two regions and each lake are given by Brezonik et al. (1983).

The 20 lakes were sampled quarterly beginning in April and May, 1978, and ending in January and February, 1979. A midlake sampling station was selected in each lake at either the deepest part of the lake or at the center of the largest basin, if the lake consisted of several basins. The same station was used on all four sampling dates.

Sampling and analytical methods for chemical parameters are described by Brezonik et al. (1983). Phytoplankton samples were collected with a 2.2-L Kemmerer bottle at 0.5 m in lakes less than 5 m deep and at the top, middle, and bottom of the water column of lakes greater than 5 m in depth. Equal volume aliquots were combined in 80-mL bottles and preserved with 2 mL of acidified Lugol's solution. In the laboratory, aliquots were settled in an Utermohl chamber and examined with a Unitron inverted microscope. Taxonomic identifications were based on keys in Whitford and Schumacher (1973), Cocke (1966), Weber (1971), Prescott (1954), and Smith (1950). All counts represent at least 200 individuals.

Zooplankton samples were obtained by vertical tow with a No. 20 Wisconsin plankton net (80-μm mesh) through the entire water column and were preserved in 10% buffered formalin. At least 100 individuals were counted for each sample under a dissecting microscope at 250×. Zooplankton biomass (milligrams C per cubic metre) was obtained by multiplying species counts by biomass conversion factors (Dumont et al. 1975). Taxonomic keys in Edmondson (1959) and Pennak (1953) were used to confirm identifications.

Descriptive statistics, correlations, and analyses of variance were calculated by the Statistical Analysis System (SAS) computer package (Barr et al. 1976). Three diversity indices (Simpson's, Shannon–Weaver, and evenness ($E = H'/H'_{\max}$)) were calculated and cluster analyses were performed with a computer package of Bloom et al. (1977). Cluster analyses were done on log-transformed data ($X' = \log(X + 1)$, where X is the abundance of a species (number per litre) in the sample). Czekanowski's index (Cormack 1971) was used as the measure of similarity between zooplankton communities in the 20 lakes.

One-way analysis of variance (ANOVA) and Duncan's multiple range test of pH data on the 20 lakes showed that they could be grouped into two nonoverlapping categories (statistically different at $P < 0.05$): an acidic group (pH < 5.3) and a nonacidic group (pH > 5.6). The two descriptors are intended to be relative terms and are used here for ease of identification. Statistically significant differences were found between mean values of many chemical parameters for the two groups (Hendry 1983). The groupings based on pH correspond fairly well to geographical groups (see Table 1), except that the three largest lakes in the Trail Ridge region (Kingsley, Geneva, and Altho) were grouped with the less acidic Highlands Ridge group. The higher pH values of the large Trail Ridge lakes probably reflect differences in shoreline cultural development and hydrologic conditions compared with the other Trail Ridge lakes.

The ensuing analysis compares planktonic population and species composition data on the two groups of lakes. To examine trends along a pH gradient in more detail, the lakes also were grouped into five categories based on divisions of 0.5 pH units as follows: pH 4.50–5.00 (four), pH 5.01–5.50 (six), pH 5.51–6.00 (two), pH 6.01–6.50 (four), and pH 6.51–7.00 (four); the numbers of lakes in each group are given in parentheses. Mean values for various biological parameters were averaged for the lakes in each category to smooth out variability among the individual lakes and clarify trends with pH.

Results and Discussion

Phytoplankton

Species richness and abundance

Mean numbers of phytoplankton species in the acidic and nonacidic lakes were 10.8 (range 8–13) and 16.5 (range 11–22), respectively. The means are significantly different (t-test, $P < 0.01$). The mean number of phytoplankton species for each lake was significantly correlated with pH ($P < 0.05$) (Fig. 1A), but considerable scatter exists in the relationship, especially for lakes with pH > 6.0. Three nonacidic lakes (Annie, Geneva, and Kingsley) had numbers of species similar to those of the acidic lakes; this trend may be explained by lower levels of total phosphorus (TP) in these lakes compared with the other nonacidic lakes.

The decrease in species numbers with decreasing pH is seen more clearly when lakes are grouped into pH intervals (Fig. 1C). One-way ANOVA and Duncan's test showed that the means of the two lowest intervals (4.5–5.5) were significantly lower than the means for the two highest intervals (6.0–7.0). Although the number of algal taxa often is greater in temperate lakes than in comparable Florida lakes, our results agree generally with those of synoptic surveys in Scandinavia (Almer et al. 1974; Leivestad et al. 1976) and Canada (Kwiatkowski and Roff 1976; Yan and Stokes 1978). These studies all show that species richness and diversity decrease with decreasing pH, and the largest changes occur in lakes with pH < 5.6.

Mean numbers of phytoplankton individuals for the 20 lakes displayed patterns similar to those for species richness. Mean abundance in the 10 acidic lakes was 5700 cells/mL (range 2900–10 900/mL), while the mean for the 10 nonacidic lakes was 14 000 cells/mL (range 4700–25 600/mL). The means are different at $P < 0.05$ (t-test). Phytoplankton abundance was positively correlated with pH ($P < 0.05$), but again the trend shows much scatter (Fig. 1B). A plot of mean abundance in the

Table 1. Summary of phytoplankton and zooplankton statistics over four quarters for 20 Florida lakes (Nos. 1–10, acidic; Nos. 11–20, nonacidic), Lake regions: T, Trail Ridge; H, Highlands Ridge.

No.	Lake region	Name	pH	Phytoplankton		Zooplankton		
				Mean No. of Species	Mean abundance (No./mL)	Mean No. of Species	Mean abundance (No./m^3)	Biomass (mg/m^3)
1	T	McCloud	4.72	12	7 300	11	79 400	116
2	T	Cowpen	4.86	9	2 900	13	30 500	24
3	T	Anderson-Cue	4.94	9	10 900	14	135 500	170
4	T	Galilee	4.98	12	5 700	17	86 400	110
5	T	Brooklyn	5.03	8	4 300	12	137 800	120
6	T	Rosa	5.06	12	3 400	13	77 900	175
7	T	Magnolia	5.10	10	5 500	15	47 300	57
8	T	Sheeler	5.14	11	3 700	12	33 200	33
9	T	Lowery	5.20	12	4 500	15	45 400	60
10	T	Johnson	5.25	13	8 500	14	79 000	64
11	H	Annie	5.75	12	8 900	16	108 900	72
12	T	Altho	6.03	17	8 700	18	70 400	49
13	H	Josephine	6.14	22	25 600	20	326 400	268
14	T	Geneva	6.15	11	4 700	18	93 500	132
15	H	Letta	6.50	19	24 500	18	150 200	92
16	H	Placid	6.54	17	9 600	17	154 300	103
17	H	June	6.67	18	9 700	21	201 600	137
18	H	Clay	6.71	18	15 100	19	38 400	120
19	T	Kingsley	6.74	12	9 100	15	109 300	66
20	H	Francis	6.80	21	24 200	23	194 300	190

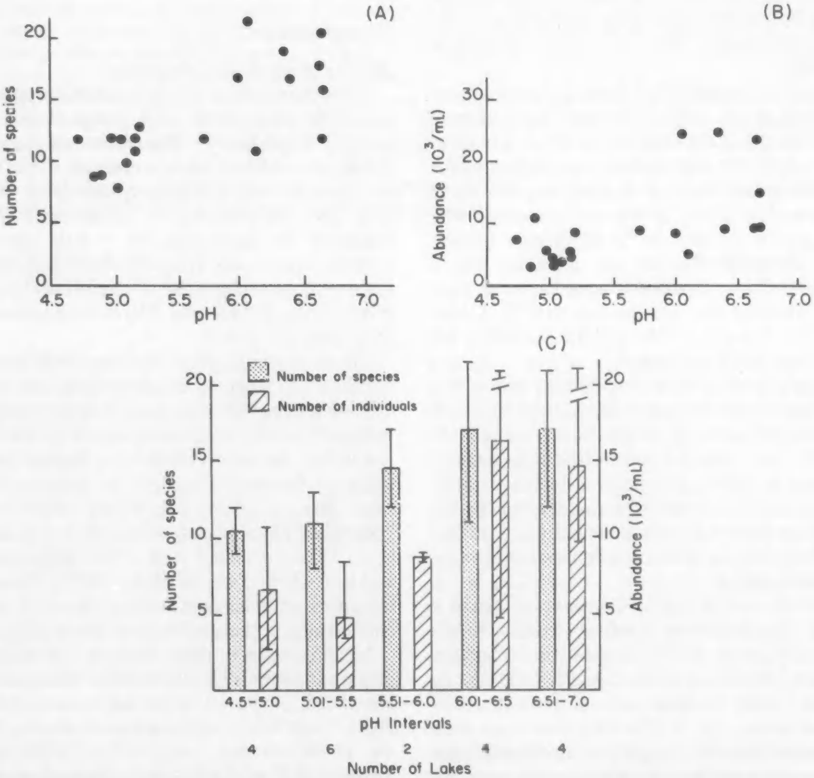

Fig. 1. (A) Mean annual species richness and (B) abundance of phytoplankton vs pH. (C) Mean values of the same parameters over 5 pH intervals. Bars denote ranges in each interval.

five pH intervals illustrates the trend more clearly (Fig. 1C). One-way ANOVA and Duncan's test showed that the means of the two lowest pH intervals were significantly lower than the means of the two highest intervals.

Scatter in the correlation between phytoplankton abundance and pH is at least partly explained by the wide range of TP concentrations found in the lakes (Hendry 1983). TP and pH both affect phytoplankton abundance (Fig. 2). A trend of increasing abundance with increasing TP levels is apparent at all pH levels but is most noticeable in the less acidic lakes. The paucity of acidic lakes with high TP levels precludes definition of the complete response surface. Phytoplankton abundance also increased with increasing pH for constant levels of TP in the data set.

Although several synoptic studies have reported trends of lower planktonic abundance with decreasing pH (e.g. Almer et al. 1974; Kwiatkowski and roff 1976), more recent reports indicate that acidification of temperate lakes is not necessarily accompanied by a significant reduction in phytoplankton biomass (Almer et al. 1978; National Research Council of Canada 1981). Several investigators (Hendrey et al. 1976; Yan and Stokes 1978) have suggested that phytoplankton biomass is controlled more by phosphorus concentrations than by pH. This hypothesis is supported by results of enclosure and whole-lake experiments in which acidic water has been enriched with phosphorus (Dillon et al. 1979; Fee 1980; Wilcox and DeCosta 1982; DeCosta et al. 1983).

Consistently low TP levels in all acidic lakes except Anderson-Cue (TP = 40 μg/L) suggest that a causal relationship may exist between TP and pH. Almer et al. (1978) suggested that nutrient cycling is diminished in acidic lakes, but other explanations are possible for the trend between TP and pH (see Hendry 1983). Acidic lakes may have lower TP input rates from both cultural and natural sources. For example, acidic lakes may have generally lower watershed to lake surface area ratios than those of nonacid lakes. Evaluation of the hypothesis that acidic lakes have lower nutrient loading rates would require accurate nutrient budget data, but such information is not available for most of the lakes. Because of the lakes' seepage character, such budgets would be difficult to determine accurately. Consequently, causes of the trends in TP and phytoplankton abundance with pH in Florida lakes remain undetermined.

Species composition

The most obvious trend in the composition of phytoplankton communities in the present investigation was a replacement of blue-green algae as the dominant group at high pH by green algae as the dominant group below pH 5.5–6.0 (Fig. 3). With the exception of an increase in pyrrhophytes (*Peridinium*) in the most acidic lakes (pH 4.5–5.0), the subdominant algal groups displayed little trend with pH. Diatoms were rare in all lakes, and no apparent trend in silica levels was evident along the pH gradient (Hendry 1983).

A decrease in the number of rare species was associated with decreasing pH (Table 2). Highly acidic lakes were dominated by *Staurastrum* sp., *Scenedesmus* sp., *Ankistrodesmus falcatus*, *Peridinium inconspicuum*, and several species of small coccoid green algae. *Euglena* sp., *Oocystis* spp., and *Chlamydomonas* sp. also were fairly common (but not dominant) in acidic lakes. Blue-green algae were sparse in acidic lakes and were represented mainly by *Oscillatoria limnetica* and *Anacystis incerta*. The less acidic lakes contained more rare species and a greater variety of blue-green species, such as *Amigdalum quadradentata*, *Anabaena* spp., *Spirulina laxissima*, and *Microcystis aeruginosa*.

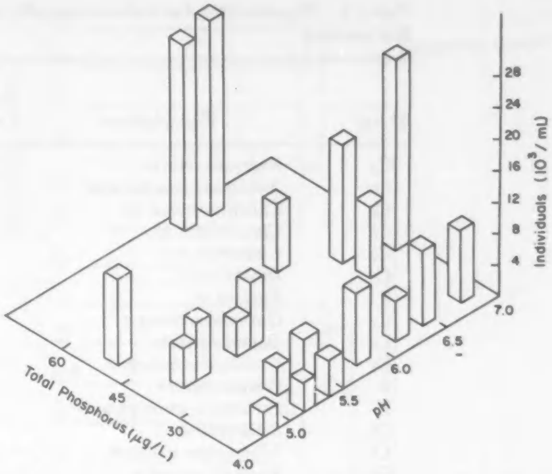

FIG. 2. Relationships among total phosphorus, pH, and phytoplankton abundance for 20 Florida lakes.

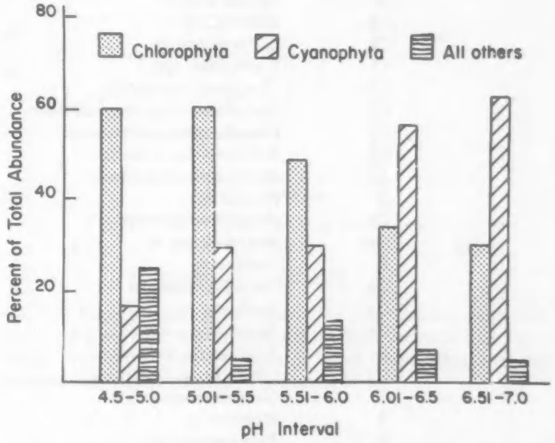

FIG. 3. Relative abundance of three major groups of phytoplankton for the 20 lakes grouped in 5 pH intervals.

Oligotrophic nonacidic lakes in Canada typically are dominated by either chrysophytes (Duthie and Socha 1976; Findlay and Kling 1979) or diatoms (Yan et al. 1977), but dominance in acidic lakes shifts to pyrrhophytes (Yan and Stokes 1978; Yan 1979). Similar trends have been reported in Sweden (Almer et al. 1974); according to Haines (1981) the same species often are dominant in acidic lakes of both countries.

Although similar taxa characterize acidic lakes in both Florida and the temperate zone, and the increased importance of *Peridinium inconspicuum* under acidic conditions is a common feature of both regions, significant differences in phytoplankton community structure are apparent. In Florida we observed a dominance of chlorophytes in acidic lakes, while pyrrhophytes, chrysophytes, and diatoms generally were of low importance across the pH range of oligotrophic lakes. Reasons for the differences in subtropical Florida lakes are not certain but may

TABLE 2. Phytoplankton distribution versus pH (× indicates species found in lake at least once during the four quarters).

Taxon[a]	Phytoplankton	pH 4.5–5.0	pH 5.01–5.5	pH 5.51–6.0	pH 6.01–6.5	pH 6.51–6.7
Cy	*Anacystis incerta*	×	×	×	×	×
Ch	*Ankistrodesmus falcatus*	×	×	×	×	×
Ch	*Chlamydomonas* sp.	×	×	×	×	×
Cr	*Chroomonas* sp.	×	×	×	×	×
Ch	*Closterium* sp.	×	×		×	×
Cs	*Dinobryon* sp.	×		×	×	×
E	*Euglena* sp.	×	×	×	×	×
Cy	*Gloeotheca linearis*	×	×			×
Ch	*Oocystis pusilla*	×	×	×	×	×
Cy	*Oscillatoria limnetica*	×	×		×	×
B	Pennate diatom	×	×	×	×	×
P	*Peridinium inconspicuum*	×	×	×	×	×
Ch	*Scenedesmus*	×			×	
Ch	*Selenastrum minutum*	×	×	×	×	×
Ch	Small gr. coccoids	×	×	×	×	×
Ch	*Staurastrum* spp.	×		×		×
Cy	*Amigdalum quadridentata*		×	×	×	×
Cy	*Anacystis montana*		×	×	×	×
B	Centric diatom		×	×	×	×
Ch	*Chlorella* sp.		×	×	×	×
Ch	*Closteriopsis* sp.		×	×	×	×
Ch	*Cosmarium* spp.		×	×	×	×
Ch	*Crucigenia tetrapodia*		×	×	×	×
Cy	*Dactylococcopis rhaphidioides*		×			
Cy	*Gomphosphaeria lacustris*		×			
Ch	*Kirchneriella contorta*		×	×	×	×
Cy	*Microcystis aeruginosa*		×		×	
E	*Phacus* sp.		×	×	×	
Ch	*Pseudotetraspora* sp.		×		×	
Cy	*Rhabdoderma* sp.		×	×	×	×
B	*Synedra* sp.		×	×	×	
Ch	*Tetradon minimum*		×	×	×	×
Cy	*Anabaena* sp.			×	×	×
Cy	*Aphanothece nidulans*			×		×
B	*Asterionella formosa*			×	×	×
Cy	*Chroococcus limneticus*			×	×	×
C	*Gonyostomum semen*			×		
B	*Melosira* sp.			×	×	×
B	*Rhizosolenia* sp.			×	×	×
Cy	*Anacystis* sp.				×	×
Ch	*Chlorogonium elongotum*				×	
Ch	*Echinosphaerilla* sp.				×	
Ch	*Elakatothrix gelatinosa*				×	
Cy	*Gloeocapsa rupestris*				×	×
Cs	*Mallomonas* sp.				×	×
Cy	*Oscillotoria angustissima*					
Cy	*Schizothrix calcicola*					×
Ch	*Staurodesmus dijectus*					×

[a] B, Bacillariophyta; C, Chloromonadophyta; Ch, Chlorophyta; Cr, Cryptophyta; Cs, Chrysophyta; Cy, Cyanophyta; E, Euglenophyta; P, Pyrrhophyta.

be related to the fact that Florida zooplankton communities are not as seriously changed by pH as those in temperate lakes. Unfortunately, our synoptic data are not sufficient to determine whether the role of zooplankton as grazers and nutrient cyclers is significantly altered by acidification.

Zooplankton

Species richness and abundance

As was the case for phytoplankton populations, the diversity and abundance of zooplankton were lower in more acidic lakes, but trends were smaller and less consistent. The mean number of zooplankton species found in the 10 nonacidic lakes was 19, while the 10 acidic lakes had an average of only 14 species; the means are significantly different (t-test, $P < 0.001$). The mean number of species in each lake also was correlated positively with pH ($P < 0.001$). Species richness over the five pH intervals (Fig. 4) increased from the second-lowest interval (5.0–5.5) to the highest interval (6.5–7.0), but ANOVA showed no signifi-

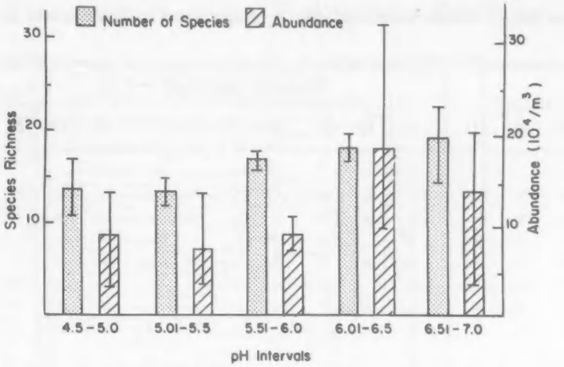

FIG. 4. Mean species richness and abundance of zooplankton in 5 pH intervals. Bars denote ranges in each interval.

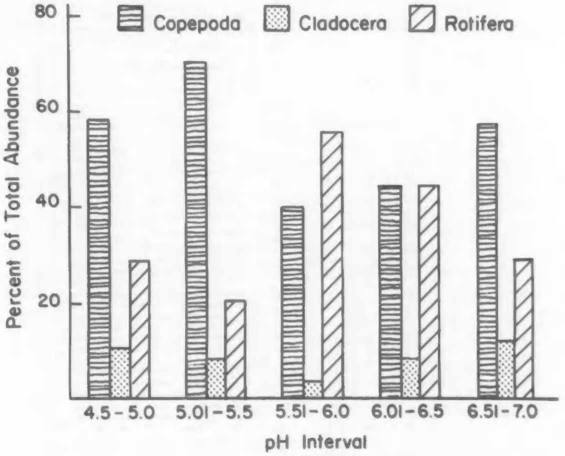

FIG. 5. Relative abundance of major zooplankton groups in 5 pH intervals.

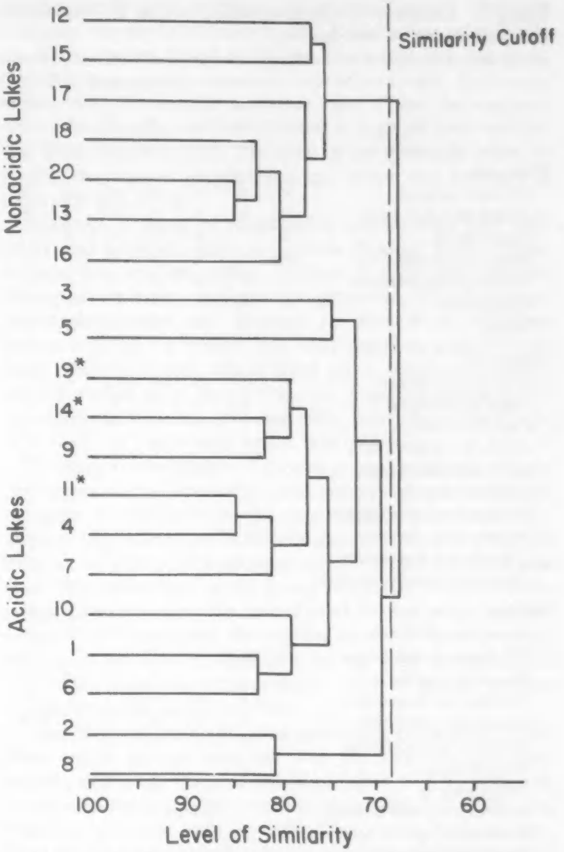

FIG. 6. Classification of 20 Florida lakes by Czekanowski's similarity index and mean annual zooplankton data (see Table 1 for key to lakes). Vertical line shows similarity level where lakes form two clusters. An asterisk indicates a nonacidic lake.

cant differences among the five groups. The range of species richness was relatively small over the entire pH spectrum, suggesting that pH does not have an overwhelming effect on zooplankton diversity in Florida lakes.

Several investigators have reported a progressive decline in numbers of species with decreasing pH in temperate lakes (e.g. Sprules 1975; Raddum et al. 1980; Confer et al. 1983), but the trend is less obvious in Florida lakes. In addition, the number of species found in the present study is much higher than numbers reported in temperate lakes of comparable pH. In a study of acidic lakes near Sudbury, Ontario, Yan and Strus (1980) found about half as many crustacean species in lakes with pH values similar to the acidic Florida lakes. Leivestad et al. (1976) reported numbers of zooplankton species in acidic Norwegian lakes that are a third to a half of those observed in this study.

Reasons for the higher diversity in Florida lakes are uncertain. Concentrations of heavy metals may be lower in Florida lakes, which are in highly weathered sandy soils compared with Scandinavian and temperate North American lakes, which are in granitic terrain. Lower concentrations of toxic metals may permit higher species diversity in acidic Florida lakes, but further studies are necessary to evaluate this hypothesis. In addition, lakes in Florida are not subjected to large seasonal fluctuations that occur in temperate lakes. The temperature range in the lakes during the year of sample collection was about 12–30°C. All the lakes are oligotrophic or mesotrophic, and none exhibited anoxic conditions in the water column. The adaptive potential of organisms to increased acidity may be enhanced by the otherwise moderate environment. Finally, lakes in the study areas probably have been moderately acidic (for natural reasons) for many years. Historical data (Hendry and Brezonik 1984) show that some Trail Ridge lakes had pH values of 5.0–5.5 more than 20 yr ago. Because the region's soil is naturally acidic and low in buffering ability, natural pH levels in many of the lakes probably were in or near this range. The high diversity of the populations thus may reflect natural selection for acid-tolerant species.

The mean abundance of zooplankton in the 10 acidic Florida lakes was 7.5×10^4 individuals/m^3 (range 3.0×10^4 to 13.8×10^4), while the corresponding value for the nonacidic lakes was 14.5×10^4 (range 3.8×10^4 to 32.6×10^4). The mean value for the acidic lakes is significantly lower than the mean of the nonacid group (t-test, $P < 0.05$). Zooplankton abundance over

TABLE 3. Composite zooplankton species list from 20 Florida lakes (see Table 1 for lake names and pH). × indicates species found in lake at least once during the four quarters.

	Acidic lakes (pH < 5.3)										Nonacidic lakes (pH > 5.6)									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Copepoda																				
Cyclops varicans	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Diaptomus floridanus	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Ergasilus sp.	×		×	×	×	×			×	×	×		×	×	×			×		
Mesocyclops edax	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Tropocyclops prasinus	×	×	×	×		×		×	×	×	×		×	×	×	×	×	×	×	×
Copepodite	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Nauplii	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Cladocera																				
Eubosmina tubicen	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Daphnia ambigua	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Leptodora kindtii	×			×	×	×		×		×	×	×	×	×	×	×	×	×	×	×
Chydorus sphaericus			×	×		×						×	×	×			×	×		
Immature cladoceran			×	×	×	×		×		×	×	×	×	×	×		×	×		×
Simocephalus sp.			×																	
Holopedium amazonicum										×										
Bosminopsis dietersi											×	×								
Ceriodaphnia reticulata																		×		
Diaphanosoma brachyurum																			×	
Rotifera																				
Keratella cochlearis	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Trichocerca multicrinus	×	×		×			×		×	×	×	×	×	×	×	×	×	×	×	×
Polyarthra vulgaris	×			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Trichocerca longiceta		×	×	×			×	×			×	×	×		×	×	×	×	×	×
Conochilus unicornis		×	×	×	×		×	×			×	×	×		×	×	×	×		×
Keratella taurocephula		×	×	×	×		×	×	×	×	×			×		×		×		×
Monostyla sp.		×				×												×		×
Kellocottia sp.				×		×		×	×	×	×	×	×	×		×	×	×	×	×
Brachionus quadridentata			×						×			×					×		×	
Monomatus sp.			×																	
Keratella quadrata				×											×					
Filinia sp.					×			×				×	×	×	×	×	×		×	×
Brachionus havanaensis							×			×			×	×			×	×		
Brachionus calyciflorus								×				×								
Pleosoma sp.									×					×						
Asplanchna sp.												×	×	×	×	×	×	×	×	×
Gastropus sp.												×								
Brachionus angularis													×		×			×		×
Platyias patulus																	×			
Conochiloides sp.																	×			
Lecane sp.																		×		

the five pH intervals displayed a somewhat inconsistent pattern (Fig. 4). The lowest population occurred in the range pH 5.0–5.5, and the highest occurred in the range pH 6.0–6.5. ANOVA and Duncan's test showed significant differences in means between pH intervals; the mean for pH 6.0–6.5 is significantly higher than the means for the two intervals from pH 4.5 to 5.5 ($P < 0.05$). The annual average (dry weight) biomass in the 10 acidic lakes was 93 mg/m^3 (range 24–175), and the average biomass in the 10 nonacidic lakes was 123 mg/m^3 (range 49–268). Biomass trends were similar to those observed for abundance, but because of large within-group variances, differences in means were not statistically significant.

Beaver and Crisman (1981) reported biomass values for ciliated protozoa in 10 of the survey lakes; their samples were collected concurrently with ours. The biomass of this often ignored zooplankton group displayed much scatter between lakes, but values generally increased with increasing pH. Although comparison with total zooplankton is limited to the acidic lake group, results indicate that ciliates are less tolerant of low pH than are other zooplankton groups. Ciliates contributed 2–7% of the total zooplankton biomass in the most acidic lakes (pH 4.7–4.9) and 20–30% in lakes near pH 5.2.

Zooplankton abundance and biomass generally decrease with decreasing pH in temperate lakes (Yan 1979; Roff and Kwiatkowski 1977; Confer et al. 1983). The latter authors found a significant correlation with pH, but Yan and Strus (1980) did not. Although pH affects the abundance of zooplankton in Florida lakes to some extent, the great variability in the data (Fig. 4) suggests that additional factors are important. For example, mean zooplankton biomass in the 20 lakes displayed a stronger correlation with chlorophyll ($r = 0.53$; $P < 0.01$) than with pH ($r = 0.25$; $P < 0.01$). Correlations using zooplankton abundance strengthened both relationships somewhat ($r = 0.62$ and 0.44, respectively; $P < 0.01$), but the trend remains. Since

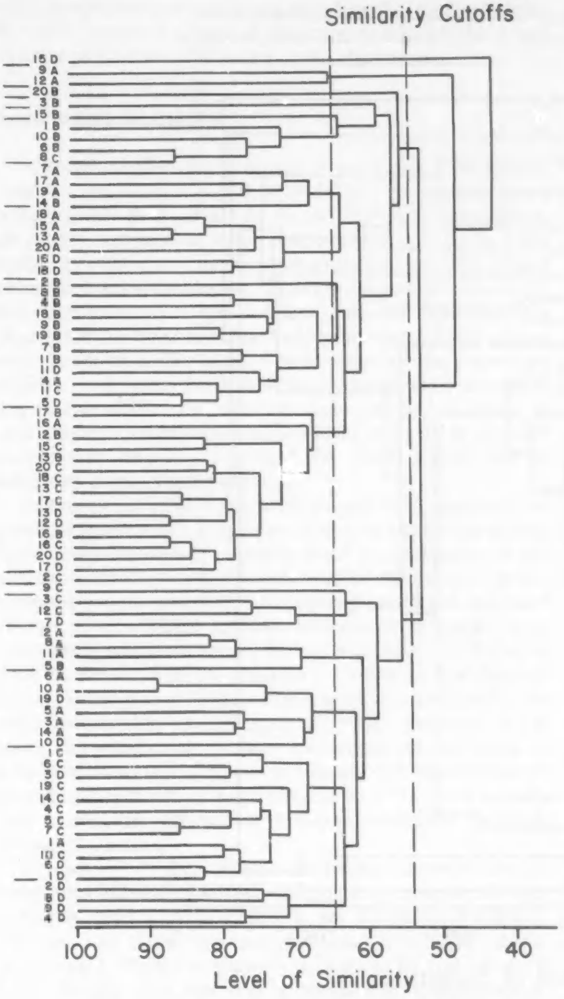

FIG. 7. Dendogram of 20 lakes based on quarterly zooplankton data (see Table 1 for key to lakes). A = spring, B = summer, C = fall, D = winter. Horizontal bars to the left denote groups formed at similarity level of 64%. Vertical lines delineate extent of clustering at two (arbitrary) similarity values.

chlorophyll levels increased with increasing pH, the modest trend between zooplankton abundance and pH may reflect changes in overall lake productivity rather than direct pH effects on zooplankton growth and survival. A similar positive correlation between zooplankton biomass and chlorophyll *a* in acidic Canadian lakes (Roff and Kwiatkowski 1977) and the pronounced response of zooplankton to fertilization of acid lakes (DeCosta et al. 1983) indicate that overall lake productivity can be as important as pH in structuring zooplankton communities in acidic lakes.

Species composition

Of considerable importance in evaluating the effects of increased acidity on zooplankton communities is the change in species composition with pH. A group of "acid-tolerant" species was dominant in all 20 lakes and consisted of *Diaptomus floridanus*, *Cyclops varicans*, *Eubosmina tubicen*, *Daphnia ambigua*, *Keratella cochlearis*, and *Mesocyclops edax* (Table 3). Other species found at all pH levels (but not dominant) included *Tropocyclops prasinus*, *Leptodora kindtii*, *Trichocera multicrinus*, *Conochilus unicornis*, and *Polyartha vulgaris*. Most of the species restricted to lakes of high pH were rotifers, and these were relatively rare even in the nonacidic lakes. A notable exception is *Asplanchna* sp., which was common in lakes with pH > 6.0.

Similarly, a group of zooplankton species dominates both acidic and nonacidic lakes in Canada (Sprules 1975). These include *Mesocyclops edax*, *Cyclops bicuspidatus thomasi*, *Diaptomus minutus*, *Holopedium gibberum*, *Diaphanosoma leuchtenbergianum*, and *Bosmina* sp. Five of the dominant genera reported by Sprules also were found in acidic Florida lakes. Daphnids were absent from acidic temperate lakes in several studies (e.g. Yan 1979), but *Daphnia ambigua* was present in all 20 Florida lakes and had a yearly mean abundance of $6 \times 10^3/m^3$ in the most acidic lake (pH 4.7).

To obtain overall trends of species composition with pH, the percentage of total species richness and abundance contributed by major zooplankton groups was calculated for each lake. Rotifers were the most diverse zooplankton group in every pH interval, but their contribution to total species richness decreased from 58% in the least acidic group to 43% in the most acidic group. Copepods were the second most diverse group in all pH intervals and displayed the reverse trend (21% of the total species at pH 6.5–7.0 and 35% of the total species at pH 4.5–5.0). Cladocerans represented 18–22% of the total number of species across all pH intervals.

Trends in relative numbers of individuals contributed by the three major groups over the five pH intervals are more complicated (Fig. 5). In acidic lakes (pH 4.5–5.5), copepods contributed the largest proportion of individuals (60–71%), and rotifers contributed only 21–30%. Cladocerans made up only 8–11% of the total abundance in acidic lakes. In the pH range 5.5–6.5, copepods declined in dominance, while rotifers increased to 46% of the total counts. The percentage contributions of the three groups in the pH range 6.5–7.0 were nearly identical to that in the most acidic interval, however. Thus, no clear trends in relative abundance of the major groups of zooplankton can be detected across the pH spectrum.

Three diversity indices were calculated from mean annual zooplankton data for the lakes. The mean values of Simpson's index (a measure of dominance) for acidic and nonacidic lake groups were 0.18 and 0.17, respectively. No differences can be discerned between the two lake groups, and dominance was rather low in both groups of lakes. The average Shannon–Weaver diversity, H', for the acidic lakes was 0.89, and the average H' for the nonacid group was 0.93, suggesting slightly greater diversity. The two groups had nearly identical evenness indices (E = 0.71 and 0.70, respectively). H' reflects both evenness and species richness, and the higher mean H' of the nonacidic lakes reflects greater species richness in this group. Overall, the similar values of the three indices for the two groups suggest that in spite of decreases in species richness little difference exists in species diversity of zooplankton communities in acidic and nonacidic Florida lakes. These results are in marked contrast with the progressive decline in diversity observed in Canadian lakes with decreasing pH (Sprules 1975; Roff and Kwiatkowski 1977).

Classification of zooplankton communities

Cluster analysis was used to identify patterns in the zooplank-

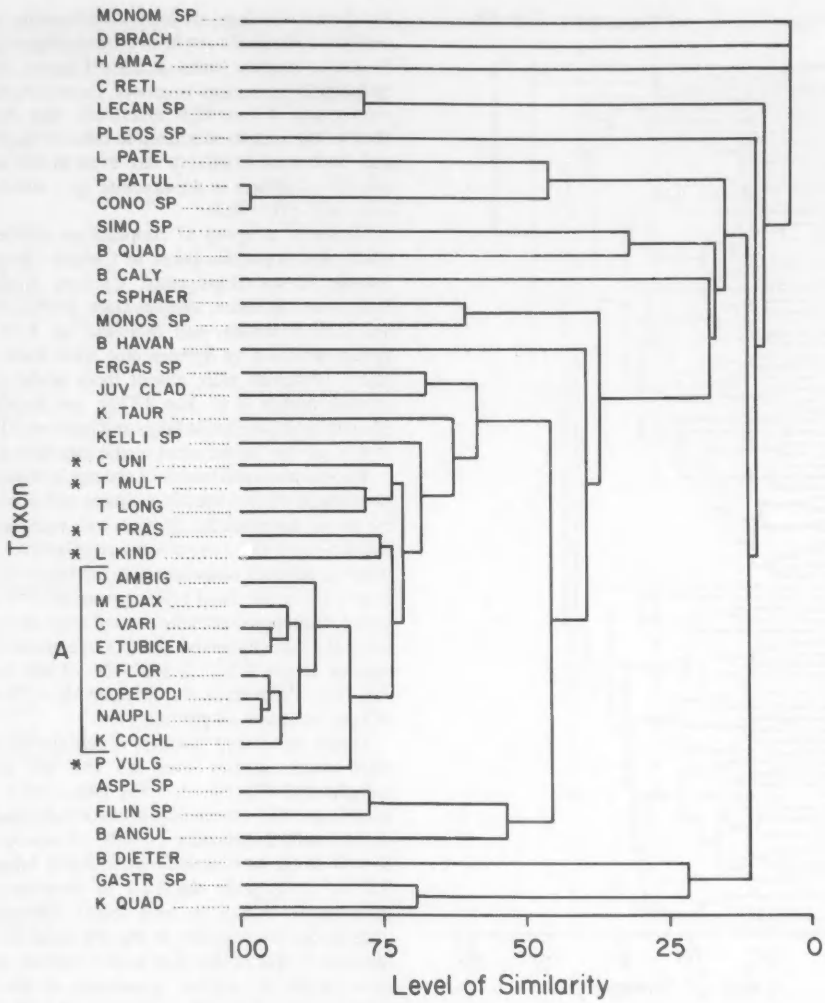

FIG. 8. Classification of zooplankton species based on mean abundance in the 20 lakes (see Table 3 for complete names of organisms). Dominant "acid-tolerant" species found in all lakes form cluster A. Species indicated with an asterisk are acid tolerant but not dominant.

ton communities in relation to pH. Two types of classification were generated: standard (Q-mode) analysis, which clustered lakes according to the similarity of species composition, and reverse (R-mode) analysis, which clustered species according to similarity of occurrence. Both analyses were performed using quantitative (actual count) data.

To assess overall trends in zooplankton communities, clustering was performed on yearly mean data. Two major groups were formed at the 68% similarity level (Fig. 6). One contains seven nonacidic lakes (pH values in the range 6.03–6.80). The second contains the 10 acidic lakes plus 3 nonacidic lakes (Geneva, Kingsley, and Annie) that are more oligotrophic than the other nonacidic lakes. This trend, along with the general trend of lower phytoplankton levels in acidic lakes, suggests that phytoplankton abundance has an important influence on zooplankton community structure.

A dendrogram also was generated from Q-mode classification of quarterly data on the 20 lakes (Fig. 7), and results show some effects of seasonality on zooplankton communities. Eleven multiobject groups (and seven single-object groups) were formed at a similarity level of 64%; these were further clustered into two main groups at a similarity level of 55%. One of the latter groups was composed primarily of acidic lakes clustered into subgroups according to a single season (fall, winter, or spring). Two low-productivity nonacidic lakes and one moderately productive, colored, and nonacidic lake also fell into this group. The second major group included clusters made up primarily of nonacidic lakes from all four quarters plus summer quarter data for the acidic lakes. Overall, the results suggest that differences exist between the acidic and nonacidic lakes during fall, winter, and spring, but their zooplankton communities are similar during summer.

R-mode cluster analysis of abundance data on species in the lakes grouped the six dominant, acid-tolerant species together with copepodites and nauplii at a high degree of similarity (Fig. 8). Other species or groups of species were added to this group in order of decreasing occurrence and abundance.

Concluding Remarks

Although trends were observed in planktonic communities over the pH range 4.7–6.8, it is difficult to separate direct effects of pH from covarying factors related to competition, predation, and nutrient status. For example, less acidic lakes tended to have higher nutrient concentrations and thus greater abundance of phytoplankton. Trends in zooplankton communities were relatively slight and less consistent than those for phytoplankton. Species richness and abundance for both groups were lower in acidic lakes. Mean values of three diversity indices, on the other hand, were nearly identical for zooplankton in the acidic and nonacidic lake groups. A group of acid-tolerant zooplankton was dominant at all pH levels, and zooplankton diversity generally was much higher than in temperate lakes of comparable pH.

Eriksson et al. (1980) attributed the increased importance of pyrrhophytes in acidic Scandinavian lakes to an increase in large herbivorous zooplankton brought about by elimination of fish and the subsequent shift to invertebrate predators. As a group, pyrrhophytes are assumed to be poorly grazed by zooplankton (Porter 1973). Major regional differences in trophic-level interactions with pH may be a reflection of the available species pool. In contrast with the situation described for Scandinavian lakes, Confer et al. (1983) noted that small species dominate the macrozooplankton assemblages of North American acidic lakes, and predaceous cyclopoid copepods are not abundant even in fishless lakes. DeCosta and Janicki (1978) attributed the importance of *Bosmina longirostris* in an acidic West Virginia lake to the near absence of a major invertebrate predator, *Mesocyclops edax*.

Regardless of cause, Florida macrozooplankton tend to be smaller bodied than those in comparable temperate assemblages (Crisman 1981). Large daphnids are absent, and *Daphnia ambigua*, one of the smallest daphnid species in North America is dominant. Predation intensity appears to be less altered in acidic Florida lakes than that in comparable temperate lakes. Total fish biomass decreases with decreasing pH in Florida lakes, but no major species replacements have been noted down to pH 4.5 (T. L. Crisman, H. Schramm, and A. Keller, unpublished data). In addition, no species of cyclopoid copepods were eliminated with decreasing pH. We suggest that the small response of zooplankton to pH, influenced by the regional absence of large-bodied species and lack of alteration in predation, may explain the dominance of chlorophytes rather than relatively inedible pyrrhophytes in the phytoplankton assemblages of acidic Florida lakes.

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Lake Mixing and Its Relationship to Epilimnetic Phosphorus in Shagawa Lake, Minnesota

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Stauffer, R. E., and D. E. Armstrong. 1984. Lake mixing and its relationship to epilimnetic phosphorus in Shagawa Lake, Minnesota. Can. J. Fish. Aquat. Sci. 41: 57–69.

Using thermometry, the mixing regime was intensively studied in each of the two principal basins of Shagawa Lake. After the thermocline had migrated past the interbasin sill depth (6m), it migrated more rapidly in the larger, windswept western basin than in the smaller, sheltered eastern basin. The metalimnetic eddy conductivities (K_z) were also larger in the west basin, ranging from $0.025 \mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ during intervals of low wind energy up to $0.25 \mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ during intervals bracketing powerful cold fronts. The bottom temperature increased rapidly in the west basin in response to mixing, reducing total water column stability and increasing susceptibility to a sudden "turnover." Because of these warm bottom temperatures and drainage basin influence, density currents sometimes carry cold water into the benthic zone of the west basin following heavy, cold rains in midsummer. Epilimnetic phosphorus concentrations in Shagawa Lake depend on linkages among weather, basin morphometry, and water column redox. Time series analysis of 8yr of record reveals the special importance of two factors. First, the anoxic zone below the mixed layer must include an important fraction of the metalimnetic shelf sediments in the western basin (6–10m zone). Second, the mixed layer must migrate downward and directly entrain water overlying the anoxic sediments. Time series analysis excludes the possibility of sediment release of phosphorus within the epilimnetic zone as the principal control on phosphorus in the pelagic mixed layer. For lakes with similar morphometry and climatic setting, and a previous history of sewage inputs, lake mixing complicates the trophic adjustment of the lake to a reduction in external phosphorus loading.

Le régime de mélange de chacun des deux principaux bassins du lac Shagawa a été l'objet d'une étude thermométrique intensive. Après la descente de la thermocline au-delà de la profondeur du seuil séparant les deux bassins (6 m), elle s'enfonce plus rapidement dans le bassin occidental, plus grand et exposé au vent, que dans le bassin oriental, plus petit et abrité. La conductivité des tourbillons métalimnétiques (K_z) est également plus grande dans le bassin occidental, variant de $0{,}025 \mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ en périodes de faible énergie éolienne à $0{,}25 \mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ dans les intervalles encadrant de puissants fronts froids. La température du fond s'élève rapidement dans le bassin occidental sous l'action du mélange, diminuant la stabilité de toute la colonne d'eau et augmentant la susceptibilité à un soudain brassage. A cause de ces températures de fond élevées et de l'influence du bassin hydrographique, les courants de densité transportent parfois de l'eau froide dans la zone benthique du bassin occidental après d'abondantes pluies froides à la mi-été. Les relations entre le temps, la morphométrie du bassin et le potentiel redox de la colonne d'eau sont des facteurs influençant les concentrations de phosphore épilimnétique dans le lac Shagawa. Une analyse d'une série de données couvrant 8 a révèle l'importance particulière de deux facteurs. D'abord, la zone anoxique sous-jacente à la couche mixte doit inclure une importante fraction des sédiments du plateau métalimnétique dans le bassin occidental (zone de 6–10 m). Ensuite, la couche mixte doit couler vers le fond et entraîner directement l'eau sus-jacente aux sédiments anoxiques. L'analyse de la série chronologique exclut la possibilité que la mise en liberté du phosphore du sédiment dans la zone épilimnétique soit le principal mécanisme de contrôle du phosphore dans la couche mixte pélagique. Pour les lacs dont la morphométrie et les caractéristiques climatiques sont semblables et qui ont reçu dans le passé des effluents d'eaux usées, le mélange complique leur ajustement trophique quand diminue la charge de phosphore externe.

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Shagawa Lake, Minnesota, has been investigated extensively concerning the relationship between lake nutrient status and nutrients received from external sources (Malueg et al. 1975; Schults et al. 1976; Larsen and Malueg 1976; Bradbury 1978; Larsen et al. 1979, 1981). The phosphorus budget studies showed conclusively that the combined lake water–sediment system had a low phosphorus retention coefficient before 1973 and became a net source of phosphorus following 1972. Larsen et al. (1981) showed that seasonal phosphorus increases in the water column correlated generally with the development of hypolimnetic anoxia during winter and summer stagnation. The authors felt that the large documented mid to late summer increases of epilimnetic total P probably were the result of upward transport from the anoxic zone; however, tentative diffusivity calculations indicated that this mechanism could not account for the observed increases.

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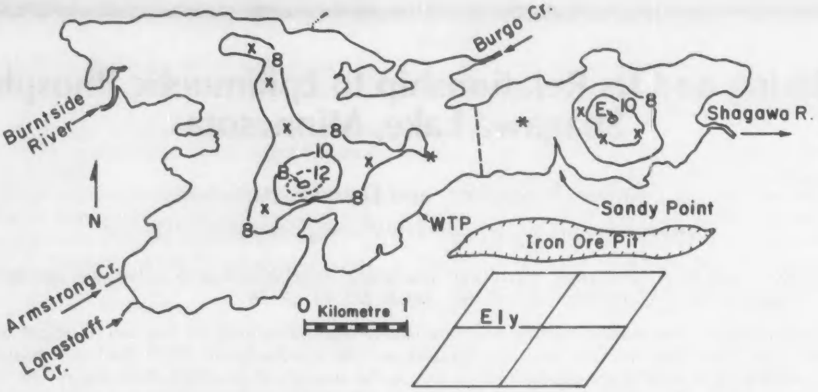

FIG. 1. Bathymetric map of Shagawa Lake showing principal influents, outlet (Shagawa River), main sampling locations at deep holes (B and E), auxiliary sampling stations (× and *), and the wastewater treatment plant (WTP). Broken line represents basin partition at narrows (for computations).

Based on Lie's (1977) studies of the epilimnetic macrophyte community, the lake's seasonal internal phosphorus supply was attributed all or in part to "macrophyte pumping" and lateral transport into the pelagic zone. Thus, until now, it has been possible to conclude only that "diverse mechanisms" are responsible for the internal supply (Larsen et al. 1981).

Based on the study by Larsen et al. (1981), and on an earlier independent investigation of Lake Mendota (Stauffer and Lee 1973), we suspected that the phosphorus economy of Shagawa Lake might be controlled by linkages among weather, lake morphometry, and redox chemistry. To better test the hydrodynamic linkage, a more rigorous description of the mixing regime and its weather correlates was required. Here, we first examine the mixing regime of Shagawa Lake in considerable detail. Following this, we show how the mixing regime is related to the redox conditions in the water column, the phosphorus economy of the mixed layer, and ultimately the trophic condition of the lake in mid- to late summer.

Site Description

Shagawa Lake is topographically aligned with a series of rocky, forested ridges up to 65 m high and interceding boggy depressions. These ridges partially shelter the lake from north and south winds blowing across the short dimension of the lake but not from the prevailing westerly winds (Fig. 1). The lake has a rocky, irregular shoreline and a small littoral zone (~7% of A_0), sparsely colonized by macrophytes. The lake is partitioned by a 6-m sill into an eastern basin with $z_{\max} = 12.5$ m and a larger (75% of A_0) western basin with $z_{\max} = 14.0$ m (Table 1). The rocky wooded islands near the narrows and the northward projecting "Sandy Point" help to shelter the eastern basin. The "Brisson Point Deep Hole" (BPDH or B in Fig. 1) and "East End Deep Hole" (EEDH or E in Fig. 1) are set in an extensive profundal plain with overlying water depths of 6–10 m. Consequently, unlike most kettle lakes, sediment contact area, $A_s(z)$, is concentrated at these intermediate depths (Fig. 2).

Tributary inflow enters the west basin; discharge occurs via the Shagawa River at the east end. The average hydraulic residence time (τ_{res}) is 0.65 yr, but most of the inflow occurs during the spring thaw (Schults et al. 1976). Because of abundant humic substances contributed by the drainage basin, the short τ_{res}, and the lake's size, light penetration does not significantly affect the metalimnetic heat flux.

The sewage waste treatment plant for the city of Ely (WTP in Fig. 1) accounted for 80% of the lake's total external P load prior to 1973 (Malueg et al. 1975). This phosphorus source was eliminated by advanced tertiary treatment beginning in early 1973.

TABLE 1. Morphometric statistics for the two principal basins of Shagawa Lake (A_0 = lake surface area (km^2); A_6 = area at depth 6 m; $\bar{z}_L$ = mean basin depth (m); $\bar{z}_6$ = mean depth of upper 6 m of basin; $\bar{z}_{6+}$ = mean depth (thickness) of water column below 6 m).

Basin	A_0	A_6	$z_{\max}$	$\bar{z}_L$	$\bar{z}_6$	$\bar{z}_{6+}$
East	2.48	1.25	12.5	5.65	4.30	2.65
West	6.76	3.95	14.0	5.95	4.75	2.00

Methods

Temperature surveys of the lake were made on 14 July 1977, during late May through mid-August 1978, and between 16 July and 18 August 1979. Either a Montedoro Whitney platinum wire thermometer (Model TCD-100B) or a combination temperature–conductance meter (M. W. model CTU-4) was used to determine temperature and/or conductance profiles from a securely anchored boat. The CTU-4 was used exclusively after June 1978. The model TCD-100B is accurate and precise to within 0.01°C; the model CTU-4 has a temperature accuracy within 0.1°C, a precision of 0.05°C, and a digital display reporting stably to 0.01°C. The temperature compensating electronics in the CTU-4 adjust in situ conductances at temperatures ranging from 5 to 25°C to a 25°C reference temperature with an accuracy exceeding ±2%.

In addition to the BPDH and EEDH positions, three satellite stations in the east basin and three to five satellite stations in the west basin (water depths ≥9 m) were visited to reduce the sampling error resulting from transient tilts and oscillations in the two basin thermoclines (cf. Fig. 1). Measurements were made at 1-m intervals within the epilimnion and 0.5-m intervals

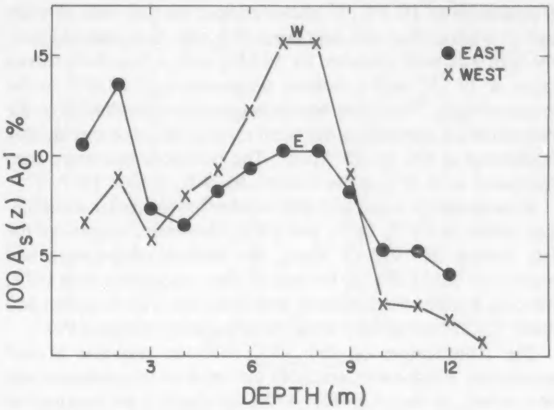

FIG. 2. Ratios of sediment contact area, $A_s(z)$, vs lake surface area (A_0) (expressed as percentage) for the two basins of Shagawa Lake. $A_s(z) = 0.5(A_{z-1} - A_{z+1})$ for z (m) = 1, 2, ...

within the metalimnion. Most of the surveys were conducted in the early morning or early evening and otherwise timed to reveal lake responses to the main weather trends (see below). Sampling errors were thus minimized following Stauffer (1982).

Wind energy and wind stress data were computed following Stauffer (1980), using the 3-h mean wind speeds and air temperatures reported by the nearest first-order weather station (International Falls, Minnesota Airport), regional seasonal norms for relative humidity, and surface water temperatures from Shagawa Lake. The airport is situated in nearly level terrain, 135 km west–northwest of the lake at an elevation of 359.4 m (48 m lower than lake surface elevation). The lake and the airport are both on the northwest side of the Mesabi drainage divide. The airport is certainly a reliable guide to winds associated with major cyclonic events. However, because of differences in topographic exposure between the airfield and the lake, the energy computations probably have more relative (day-to-day contrasts) than absolute significance.

Where important, precipitation over the Shagawa Lake drainage basin was estimated by averaging NWS data reported for Winton Power Plant (47°56′N, 91°46′W) and Tower (47°45′N, 92°17′W). The geographic center of Shagawa's drainage basin is close to 47°55′N, 91°58′W.

The free convective circulation depth at time t, here denoted $h_c(t)$, is that point in the water column (z measured positively downward from the lake surface) above which $\Delta\rho/\Delta z \leq 0$ for all $z < h_c(t)$. After the water column warms beyond 4°C, this inequality is equivalent to $\Delta T/\Delta z \geq 0$ for all $z < h_c(t)$. The maximum convective circulation depth during any time interval (t_1, t_2) is denoted $h_c^{\max}(t_1, t_2)$. The maximum overnight value of h_c for a given Julian day is denoted $h_c^{\max}$(J.D.). During typical summer weather, the latter can be estimated by simple inspection of the early morning temperature profile (prior to the onset of daytime heating). Alternatively, if sampling was conducted in the afternoon, $h_c^{\max}$(J.D.) can be estimated approximately by "subtracting" ~250 cal·cm^{-2} from the upper portion of the temperature profile, subject to the constraint that the resulting "mixed layer" is left isothermal. The accuracy of this procedure is improved if night-specific estimates of nocturnal heat losses are available instead of just seasonal average values (Stauffer 1982; R. E. Stauffer, unpublished data).

The above definitions assume that any "point estimate" of $h_c(t)$ over the lake surface is representative of the whole lake. For Shagawa Lake this assumption is violated because the thermoclines migrate at different rates in the two basins (see below). For this lake it is convenient to define a basin-weighted lake-average overnight convective circulation depth, denoted $\bar{h}_c^{\max}$(J.D.), using 0.75 and 0.25 as statistical "weights" for the west and east basins, respectively. These weights are proportional to the respective surface areas and nearly proportional to basin areas at intermediate depths (Table 1). Thus, because the thermocline migrates more rapidly in the west basin, a hypothetical value, $\bar{h}_c^{\max}(215)$ = 9.5 m might typically represent a maximum mixed layer thickness of 10.0 m in the west basin coupled with 8.0 m in the east basin on Julian day 215. It is important to emphasize that this averaging procedure has nothing to do with thermocline tilt accompanying wind setups or temperature seiching; the two main basin thermoclines tilt separately after $\bar{h}_c^{\max}$ has migrated past the 6-m interbasin sill depth. The tilt effects are separately removed by areal averaging within basins. The lake-mean estimator is employed to condense more detailed information for presentation in this paper.

One importance of the parameter $h_c^{\max}(t_1, t_2)$ is that unbiased estimates of the vertical eddy conductivity, $K_z(t_1, t_2)$, can only be calculated (independently for each basin) using the flux-gradient algorithm during the time interval (t_1, t_2) for depths: $z > h_c^{\max}(t_1, t_2)$.

The basin-specific eddy conductivities were calculated using an improved flux-gradient algorithm (cf. Jassby and Powell 1975 for basic equations) that models the depth-dependent changes in sediment heat storage in addition to water column heat storage (Stauffer 1982). Following Stauffer (1982), the lake "revisit technique" was used to minimize the effects of sampling errors on K_z and also to provide estimates of uncertainty for this important parameter.

A redox estimator, $R_z(t)$, is here defined as that depth below which the sediment–water interface is anoxic during intervals of thermal stratification. Here, $R_z(t)$ was equated with the depth of the 3 mg·L^{-1} isopleth at stations BPDH (west basin) and EEDH (east basin). The 3 mg·L^{-1} isopleth was selected because lake surveys in 1978–79 showed that a ~50-cm benthic interval above the extensive metalimnetic shelf sediments was anoxic at times when ~3 mg O_2·L^{-1} remained at the same depth in the neighboring "deep hole" position. These surveys were performed using the in situ conductance meter and noting the conductance shift near the shelf sediments corresponding to the appearance of Mn^{2+} and Fe^{2+}. A second reason for selecting the 3 mg·L^{-1} isopleth as a redox marker was that its position is insensitive to measurement errors (both variable analytical biases at low oxygen concentrations, and the small oxygen gradients at low concentrations). The oxygen concentration gradient is typically so steep in the metalimnion of this lake that the use of any oxygen isopleth between 2 and 4 mg·L^{-1} leads to essentially the same redox marker, $R_z(t)$. Furthermore, in other lake studies (R. E. Stauffer, unpublished data) the benthic boundary layer above metalimnetic shelf sediments was found to have lower oxygen concentrations (by 1 to several mg·L^{-1}) as compared with adjacent deepwater profiles.

The lake-mean value for $R_z(t)$, denoted $\bar{R}_z(t)$, was calculated using the same basin weights (0.75 west, 0.25 east) applied to the analysis of mixed layer depth.

The precision of the estimates $\bar{h}_c^{\max}$(J.D.) and $\bar{R}_z$(J.D.), calculated for the earlier years (1971–77) based on data provided by the USEPA, is relatively low ($\hat{\sigma}_z \sim 0.50$ m). During those earlier years usually only two stations were visited (BPDH and EEDH), and parameters were measured at 1.5-m intervals throughout the water column. Furthermore, variable weather conditions during sampling certainly introduced sampling error, particularly associated with thermocline tilts in the asymmetric western basin. Consult Larsen et al. (1979; 1981) and Larsen and Malueg (1976) for additional details on earlier sampling. The precision of our 1978 estimates is higher ($\hat{\sigma}_z \sim$ 0.25 m) because of the systematic sampling design conditioned on antecedent weather (cf. Stauffer 1982).

Results

Weather Time Series

As in Madison, Wisconsin, the spring weather in northern Minnesota is characterized by extreme year-to-year variability and long statistical "runs" of low wind energy (cf. Stauffer 1980). As a consequence, observed conditions in Shagawa Lake often reflect weather departures from normal.

The windpower time series during summer is subject to greater extremes in northern Minnesota than in southern Wisconsin. This regional difference is part of a continental trend extending from the Canadian border down the Mississippi Valley lowland to the Gulf of Mexico at this time of year (R. E. Stauffer and N. D. Dominguez, unpublished data) and is probably a consequence of the northward seasonal shift in cyclonic storm tracks.

Details of the air temperature and windpower time series during the late spring and summer of 1971 and in 1974–78 are shown in Fig. 3. A cold front during Julian days 205–206 (1971) delivered $8.3 \times 10^3\,\mathrm{J \cdot m^{-2}}$ and was accompanied by an air temperature plunge to 2°C on the night of day 208. Both the maximum 3-h wind stress, τ (cf. Stauffer 1980 for equations), and the input of mechanical energy were nearly double the maximum comparable summer inputs for Lake Mendota, Madison, Wisconsin, during the last 15 yr of records (Stauffer 1980; R. E. Stauffer, recent unpublished data). Other important "events" include days 207–210 in 1974 ($10.4 \times 10^3\,\mathrm{J \cdot m^{-2}}$, with a minimum overnight air temperature of 7°C), and days 163–166 in 1976 ($8.5 \times 10^3\,\mathrm{J \cdot m^{-2}}$). The cold front during late August 1976 delivered less energy but was accompanied by minimum air temperatures of 2°C.

In other summers the maximum wind energy inputs are smaller than in 1971, 1974, or 1976, but the sequence of alternating warming and cooling trends remains as a salient climatic feature.

Onset of Thermal Stratification

In Mays featuring both cool and windy weather the onset of stratification was delayed until June. Thus, following a near-normal ice-out in early May 1971, near-normal air temperatures and high late May windpower (Fig. 3) resulted in a nearly isothermal water column on 1 June and a bottom temperature of 10.5°C in the western basin. Even warmer bottom temperatures were observed at the end of May 1973 (12.0°C) in response to both high May windpower and an earlier than normal ice-out (mid-April).

In other years unseasonably warm and windless periods in May caused early onset of thermal stratification. For example, after an early April ice-out in 1977 (premature by ~1 mo), the period 11–28 May featured both low windpower and a mean air temperature of 19.7°C, 9° above normal for that time of year, and 1° warmer than the July norm (Fig. 3). As a consequence, the lake was fully stratified by 24 May with a 3-m-thick mixed layer at 18.2°C and a bottom temperature of 11.0°C in the western basin. The warm bottom temperature resulted from the premature ice-out and earlier wind mixing (the lake was already isothermal at 6°C by 25 April). The bottom temperature then increased to 12.0°C in the western basin by 7 June 1977.

Unseasonably warm and still weather led to similar stratification onsets in 1972, 1976, and 1978. However, because of the late ice-out in 1972 (9 May), the bottom temperature had warmed to only 6.0°C by the end of May. In contrast with 1977, the cold bottom temperatures stabilized the water column and made it resistant to deep wind mixing during summer 1972.

The stratification on day 147 (1978) in response to low antecedent windpower, and both elevated air temperatures and dew points, is shown in Fig. 4. Notice that (1) the bottom 6 m are nearly isothermal at different temperatures in the two basins, (2) a sharp thermocline extends to the lake surface, and (3) the warmest surface water is in the east basin, although this basin was sampled first, and prior to an opportunity for daytime heating.

The warmer surface waters in the east basin resulted from advection by light northwest breezes during the 18 h preceding sampling. The temperature profiles below 2 m resemble negative exponential heating curves caused by light absorption in humic stained water, superimposed on previously isothermal water columns at 8.75 and 9.5°C. These temperature profiles could not have been affected by recent inflows because regional precipitation had been only 50% of normal following March and 30% below normal for the winter.

Summer Stratification

After the onset of stratification, wind energy, air temperature, humidity, and solar radiation act in concert to regulate the heat budget and the convective circulation depth in each basin. The dynamics of this process have been described for other lakes (Octavio et al. 1977; Ford and Stefan 1980; Stauffer 1982). Here, we illustrate the dynamic regulation of the thermocline by weather fronts during early summer 1978. We show why these "events" have both immediate and delayed consequences for the lake.

Partly because of the initially shallow thermocline, Shagawa Lake responded dramatically to the energetic cold front that followed day 148 in 1978 (Fig. 3). Large heat gains were registered below the 3 m level and extended all the way to the bottom, particularly in the west basin (Fig. 4). By day 164 a true hypolimnion (near-isothermal depth interval below the thermocline) no longer existed because of metalimnetic displacement to deeper depths accompanying the cold front. The mixed layer thickened and cooled because of the downward heat flux; however, the lake actually gained $850\,\mathrm{cal \cdot cm^{-2}}$ between days 147 and 164.

The upper portions of the temperature profiles from 164-a.m. show the effects of strong surface heating accompanying near-calm, sunny weather. However, at 19:30 (CST) the previous evening, h_c was 4.5 m in each basin. A detailed comparison shows that overnight heat losses occurred down to 6.5 m and totaled $225–250\,\mathrm{cal \cdot cm^{-2}}$ at each station. These losses probably resulted from localized convective circulations set up by surface heat losses during the calm, clear, cold (~7°C minimum) night terminating a cold front cycle. These heat

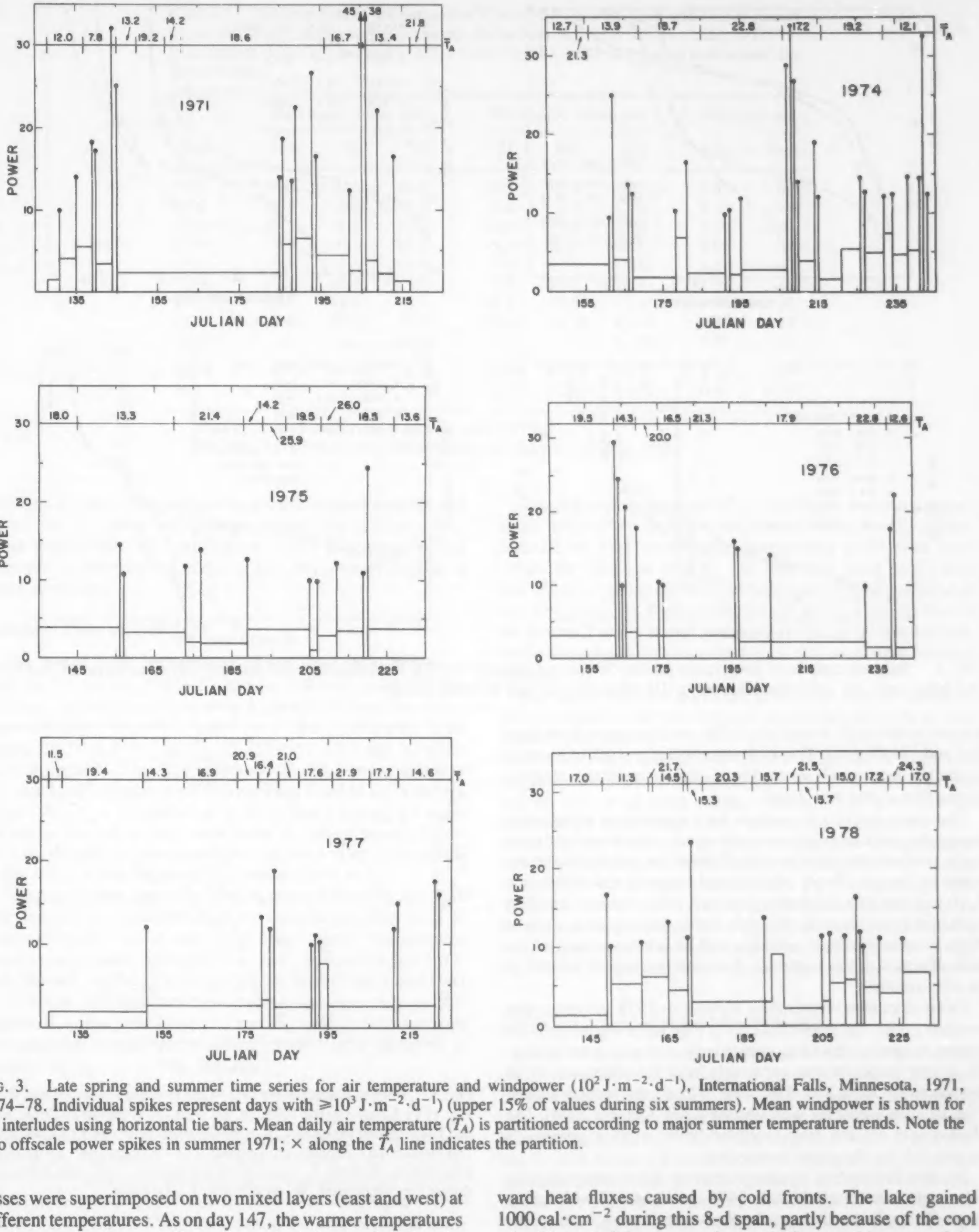

FIG. 3. Late spring and summer time series for air temperature and windpower ($10^2\,J\cdot m^{-2}\cdot d^{-1}$), International Falls, Minnesota, 1971, 1974–78. Individual spikes represent days with $\geq 10^3\,J\cdot m^{-2}\cdot d^{-1}$) (upper 15% of values during six summers). Mean windpower is shown for all interludes using horizontal tie bars. Mean daily air temperature ($\bar{T}_A$) is partitioned according to major summer temperature trends. Note the two offscale power spikes in summer 1971; × along the $\bar{T}_A$ line indicates the partition.

losses were superimposed on two mixed layers (east and west) at different temperatures. As on day 147, the warmer temperatures in the east basin at 163-p.m. resulted from advection by antecedent westerly winds.

The most energetic cold front of May–August 1978 occurred during days 170–172 (Fig. 3). Temperature profiles from dates bracketing this event (164 and 174) again illustrate the downward heat fluxes caused by cold fronts. The lake gained 1000 $cal\cdot cm^{-2}$ during this 8-d span, partly because of the cool mixed layer left by the previous cold front and because of the above-normal air temperature (21.7°C) preceding the clockwise (south to northwest) wind shift during the day 170–172 cold front.

Unlike conditions on days 147, 163-p.m., and 164-a.m., the

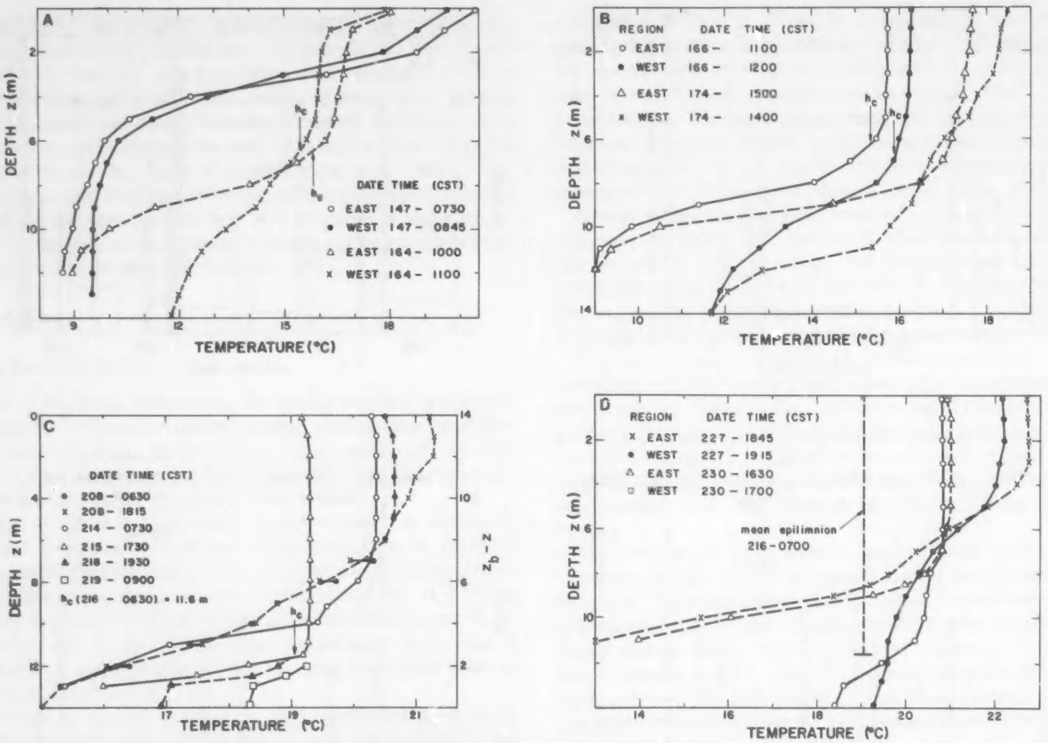

FIG. 4. Shagawa mean basin temperature profiles for selected intervals in 1978. (A) Julian days 147 and 164; (B) Julian days 166 and 174; (C) Julian days 208–219 (west basin only); (D) Julian days 227 and 230 (both basins).

warmer epilimnetic water was in the west basin on both days 166 and 174 (Fig. 4). This difference was the result of easterly or southeasterly winds on the day of, and day prior to, sampling during these latter two dates.

The above analysis shows how $h_c(t)$ increases to a maximum during the cold clear night terminating each important cold front cycle and how the cyclical wind shifts affect interbasin surface water exchange. Theory predicts and experience confirms that $h_c(t)$ migrates upward during the sunny calm weather identified with high-pressure cells (Stauffer 1980). During June, each of these weather cycles is accompanied by a net warming of the lake. Because of this warming, $h_c(t)$ rarely migrates below 7 m in early summer.

From extensive temperature surveys in 1978 we know that weather cycles are responsible for a very rapid warming of the bottom waters in this lake, particularly in the west basin (Fig. 5). Severe thunderstorms apparently have this effect as well, as evidenced by days 176–179 (day 177 had the second highest "fastest mile" (from the west) during April–October 1978). The shallowness of the lake, coupled with wind exposure, is responsible for this rapid heating rate.

Neither the bottom temperatures nor the monthly heating rates were particularly high in 1978, as compared with earlier years (Table 2). In all years the rates were higher for the west basin.

From comparative studies on Wisconsin lakes (R. E. Stauffer, unpublished data), we estimate that the expected midsummer "equilibrium surface temperature" (energy balance with the atmosphere) for Shagawa Lake is 20.8 ± 0.5°C, e.g. about 2° above the mean July air temperature. Because of the short summer at this latitude, the expected equilibrium temperature is ~4° colder by the end of August. Thus, the bottom temperatures in the west basin rapidly converge toward the equilibrium surface temperature (Table 2; Fig. 5). The process of bottom

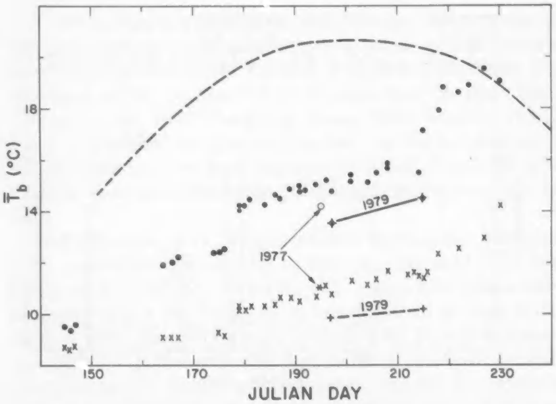

FIG. 5. Bottom temperatures ($\bar{T}_b$) in the two deep holes (B and E in Fig. 1) vs Julian day for 1978. In the west, $\bar{T}_b$ is the mean of the 12- and 13-m values; in the east, $\bar{T}_b$ is the mean of the 11- and 12-m values. The broken line denotes the approximate "equilibrium" epilimnion temperature. Several $\bar{T}_b$ values from midsummer 1977 and 1979 are shown for comparison. ●, west basin; *x*, east basin.

TABLE 2. Summer bottom temperatures (°C at 12.5 m in west basin and 11.5 m in east basin) and heating rates (degrees per month, Julian days 151–212) Shagawa Lake, 1971–79. Temperature values interpolated to Julian days 151, 181, and 212 (ignoring extra winter day in leap years).

	East basin, Julian day			West basin, Julian day			Heating rates	
Year	151	181	212	151	181	212	East	West
1971	9.2	10.5	10.9	10.5	13.8	16.5	0.85	3.00
1972	5.1	6.2	7.1	6.4	9.2	11.8	1.00	2.70
1973	11.3	13.6	15.7	12.0	16.9	17.8	2.20	2.90
1974	9.0	9.5	10.9	9.5	12.0	14.5	0.95	2.50
1975	6.9	8.8	9.5	9.9	12.0	15.1	1.30	2.60
1976	10.4	12.4	14.2	11.5	14.1	16.4	1.90	2.45
1977	10.1	11.0	11.1	11.5	13.0	15.1	0.50	1.80
1978[a]	8.81	10.31	11.50	10.14	14.52	15.61	1.35	2.75
1979[a]	—	—	10.09	—	—	14.36	0.55	1.80
Mean	8.85	10.30	11.20	10.20	13.20	15.25	1.25[b]	2.60[b]
SD	2.00	2.25	2.50	1.75	2.25	1.70	0.55	0.35

[a] Data by R. E. Stauffer; EPA data for years 1971–77.

[b] Omitting 1979 rate (extrapolated from Julian days 197–215 in 1979).

warming by eddy diffusion reduces water column stability and leaves the west basin increasingly susceptible to each subsequent wind event. This process can result in premature "fall turnover" of the west basin during late July or early August of some summers.

Turnover: Early August 1978

The mixed layer temperature of the west basin decreased from 21.2°C on day 208 to 20.35°C at 214-a.m. to 19.30°C by 215-p.m., accompanying an early August cold front. The mixed layer boundary migrated from 8 to 11.5 m in the west basin during the final 34 h (Fig. 4). At 215-p.m. the water temperatures at 0 and 11.5 m were identical (19.18°C) and colder than the bulk water column (19.30°C) between 2 and 11 m. Although lapse ($dT/dz > 0$) prevailed in the upper 11 m of the water column, temperature increases were occurring rapidly below 11.5 m. Bottom temperatures then continued to increase rapidly in the 4 d of a warming trend following 216-a.m.

The mixed layer depth was sharply reduced between 216-a.m. and day 227 in response to an air temperature shift from 8° below the early August norm to 8° above norm. The warming trend caused reestablishment of a "new" epilimnion at 22.8°C that "floated" on the 19°C water that had formed the mixed layer at 216-a.m. Because the new thermocline was only weakly stabilized, a new wind storm and cooling trend quickly destroyed the temporary stratification. This process also occurred in August 1971.

Density Currents

Between days 227 and 230 the mixed layer in the western basin cooled to 20.85°C in response to a cold front. Although $h_c^{\max}(227, 230)$ cannot have exceeded 9 m during this interval, and significant heat gains were registered between 8 and 11 m in the western basin, the bottom 1.5 m of the water column in the western basin lost an average of 0.85° (Fig. 4). By contrast, significant heat gains were registered at all depths below $h_c^{\max}(227, 230)$ in the east basin. What accounts for these anomalous heat losses in the benthic boundary layer of the west basin accompanying this cold front?

Rain fell during this interval (6.5 cm total) and accompanied an air temperature shift to a minimum 11°C in the Ely region. Because the minimum bottom temperature in the west basin before the rain was 19.5°C, the cold rain could easily have resulted in a "plunging inflow" to the west basin (cf. Fischer et al. 1979, Chap. 6). By contrast, bottom temperatures in the east basin were initially lower, and that basin lacks tributaries; here, temperature gains by downward eddy diffusion were recorded instead.

The above analysis illustrates that under certain conditions the one-dimensional assumptions underlying all vertical flux-gradient calculations (K_z) are seriously violated in the west basin (the eddy conductivity in the bottom 2 m cannot be negative). Both the large land drainage to west basin area ratio and the very small basin volume at depths >10 m increase the potential for these large-scale "convective circulations." Furthermore, the potential for these occurrences increases after mid-July, both because of the atmospheric cooling and cumulative bottom warming after midsummer. By contrast, basin-wide convective circulations set up by severe nocturnal cooling in the littoral zone are unlikely to be significant because of the very small littoral zone. During rainy summer intervals with "plunging inflows," the K_z estimates for the west basin are biased low.

Eddy Conductivities in the Metalimnion

Table 3 contains the sine wave parameters used for modeling sediment–water heat exchange in the two basins of Shagawa Lake. For the west basin the depth-dependent sine period corresponds to a maximum temperature at the sediment–water interface on day 212 (31 July) in the depth interval 0–7 m and on day 217 (15 August) at 12 m. Both the timing and amplitudes of the temperature shifts are thus representative of the west basin. The longer periods and smaller amplitudes for the east basin reflect the delayed and weaker temperature pulses in the wind-sheltered deeper waters. Complete turnover in that basin depends mainly on late summer cooling of the mixed layer.

The effect of the modeled sediment heat exchange on K_z estimates for two important and representative time intervals in 1978, e.g. in mid-June and late July, is shown in Table 4.

TABLE 3. Sediment sine wave heat exchange parameters for the Shagawa Lake eddy diffusivity model (see Stauffer 1982). Minimum sediment heat content on Julian day 75 (all depths, both basins).

Depth z (m)	Period (Julian days)[a] East	Period (Julian days)[a] West	Amplitude (degrees) East	Amplitude (degrees) West
4	274	274	9.5	9.5
6	274	274	8.5	8.5
7	274	274	8.0	8.0
8	290	284	7.7	7.7
9	305	294	7.5	7.5
10	320	304	7.0	7.2
11	335	314	6.5	7.0
12	350	324	6.0	7.0

[a] Sine wave period for spring–summer sediment heating cycle (depth dependent because of stratification).

[b] Half the mean annual fluctuation in lake water temperature adjacent to sediment at depth z.

TABLE 4. Eddy diffusivity rates, K_z ($\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$), in Shagawa Lake's west basin calculated using two flux-gradient algorithms. Model 1 values calculated using sediment heat exchange parameters listed in Table 4. Model 2 values assume no sediment heat exchange.

Depth z (m)	Julian days 166–174 Model 1	Julian days 166–174 Model 2	Julian days 208–214 Model 1	Julian days 208–214 Model 2
6	0.255	0.182	—	—
7	0.188	0.122	—	—
8	0.127	0.082	0.047	0.033
9	0.152	0.105	0.080	0.057
10	0.113	0.085	0.024	0.011
11	0.052	0.033	0.016	−0.006
12	0.038	0.009	0.016	0.005

Changes in sediment heat storage increase the flux gradient K_z estimates by 0.07 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ at 6 m during mid-June. The magnitude of difference in June then changes little with depth until 10 m but drops to 0.03 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ at 12 m; the difference is sensitive to the basin-specific ratio of sediment contact area to water volume at each depth. The differences between the two algorithms narrow by late July because of the slowing rate of heat penetration into the sediments during the late part of the heating cycle. The model differences depend on depth and Julian date interval; they are independent of the short-term heating rate of the water column itself, except insofar as it effects temperature gradients. Thus, during relatively quiescent periods featuring low transport rates in the water column, the difference between algorithms is an important fraction of the sediment-adjusted K_z estimates. Conversely, during short periods of highly accelerated transport (e.g. days 214–215) the differences between the two algorithms are much smaller than the uncertainty in K_z contributed by sampling error in the lake temperature surveys (see below). The sediment–water exchange of heat is particularly important in this lake, both because of the fluidity of the sediments and the large amplitudes of the seasonal temperature variation at all water depths.

The precision of the K_z estimates is always difficult to specify exactly because it depends on so many factors, e.g. lake basin size and configuration, seiche damping rates, sampling design, water column stability, and antecedent weather at the time of sampling (cf. Stauffer 1982).

Based on the usual sampling design for each Shagawa basin, and applying the "revisit technique" (Stauffer 1982), the estimated precision (1 $\hat{\sigma}_k$ value) for the metalimnetic K_z estimates is 0.11 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ in the western basin and only 0.03 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ in the eastern basin. These errors apply to 24-h intervals. As the time interval lengthens, the errors decrease as $\hat{\sigma}_k / \Delta t$ (Δt in days) until the temperature gradient portion of the total error begins to dominate statistically (after about 2 wk during typical summer weather). Even for longer intervals the gradient-related error component is less serious because this component is negatively correlated at adjacent depths (Stauffer 1982).

For the 8-d interval spanning days 166–174 (1978) the estimated error in K_z below 8 m is ~0.015 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ in the west basin and ~0.005 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ for the east basin. Conversely, during the 34-h time interval ending on day 215 the estimated uncertainty at 12 m in the western basin is at least 0.08 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ and probably higher because high wind energy and low water column stability immediately preceded day 215. It is thus clear that the relative error becomes uncomfortably large for sampling intervals shorter than a few days, particularly if eddy diffusion has been slow during this date period. The experimental design easily allows estimation of K_z values for weather cycles of ~1-wk duration.

The vertical eddy conductivities in the main thermocline depend on depth, wind energy, wind exposure, and water column stability. The transport rates are thus highly basin dependent (Table 5).

During 10 Julian date intervals between 27 May and 4 August 1978, K_z in the middle to upper portion of the main thermocline ranged from 0.02 to 0.25 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$ in the west basin and was generally much lower in the wind-sheltered east basin (range 0.002–0.14 $\mathrm{cm}^2 \cdot \mathrm{s}^{-1}$) (cf. Table 5). The eddy diffusivities correlate well between the two basins and were generally markedly higher during the time intervals with higher regional windpower. This power relationship breaks down for days 176–179 when severe thunderstorms were moving through northern Minnesota on two successive days.

After the deep penetration of the mixed layer on 216-a.m., the K_z values at intermediate depths were much larger in the west basin than in the east basin. This was a result of the comparatively low water column stabilities in the west basin accompanying the new warming trend (Table 5).

The "local" water column stability or Brunt Väsälä frequency (parameterized as $N_z^2(t)$) is both a cause and a consequence of the different eddy diffusion regimes in the two lake basins (Table 5). As shown by Quay et al. (1980), Jassby and Powell (1975), and others, increasing $N_z^2(t)$ normally suppresses K_z because the buoyancy forces resist eddy displacement. However, in Shagawa Lake the different stabilities are also a consequence of different mixing intensities because both basins begin the heating period in identical condition and are subjected to the same external thermal balance. Thus, the mixing regime is "feedback controlled" as shown by the August comparative data. This is also the message of the sharply diverging bottom water heating rates in the two basins (Fig. 5; Table 2).

TABLE 5. Eddy diffusivities and water column stabilities, Shagawa Lake thermocline, 1978.

Julian date interval	Final lake mean temperature (°C)	Mean windpower ($10^2\,J\cdot m^{-2}\cdot d^{-1}$)	z (m)	K_z ($cm^2\cdot s^{-1}$)		$N^2(z)$ ($\times 10^4$ cgs units)[a]		Total stability ($g\cdot cm^{-3} \times 10^4$)[b]	
				East	West	East	West	East	West
147–164	15.83	6.5	8	0.057	0.245	11.6	3.7	14.2	11.6
164–174	17.48	7.3	8	0.045	0.130	22.5	8.0	11.3	7.4
176–179	19.00	1.7	7	0.137	0.144	11.6	5.4	14.1	9.6
179–184	19.01	2.9	7	0.015	0.023	15.2	11.7	14.5	9.4
184–191	19.40	4.8	7	0.002	0.050	24.4	15.5	15.1	9.0
191–196	19.80	6.5	7	0.046	0.077	30.7	12.8	16.3	8.5
196–204	20.20	2.4	7	0.002	0.022	26.0	13.5	16.6	9.5
204–208	20.46	7.5	7	0.089	0.123	26.9	12.4	17.1	9.1
208–214	20.06	5.1	8	0.006	0.047	20.0	6.2	16.0	7.9
214–215	18.86	19.5	9[c]	0.040	0.210	52.3	20.0	12.9	4.7
216–219	20.10	6.3	9	0.027	1.180	47.4	0.6	13.3	2.1
219–222	20.02	5.3	9	0.027	0.195	47.4	1.5	13.3	2.4
222–227	21.58	5.8	9	0.010	0.125	39.0	3.6	16.4	3.7
227–230	20.63	9.8	9	0.035	0.245	38.6	3.5	15.0	4.2

[a] Local stability.

[b] Density difference between surface and bottom; average for Julian date period.

[c] 11.5 cm in west basin.

TABLE 6. K_z and water column stabilities for the two Shagawa Lake basins, Julian days 197–215, 1979.

	East				West			
Depth, z ($cm^2\cdot s^{-1}$)	K_z ($cm^2\cdot s^{-1}$)	N_z^2 ($\times 10^3$)	$K_z \times N_z^2$ ($\times 10^5$)	$K_z \times N_z$ ($\times 10^5$)	K_z ($cm^2\cdot s^{-1}$)	N_z^2 ($\times 10^3$)	$K_z \times N_z^2$ ($\times 10^5$)	$K_z \times N_z$ ($\times 10^5$)
6	0.0364	2.29	8.35	5.51	0.0281	2.64	7.42	4.57
7	0.0143	4.84	6.92	3.51	0.0185	3.13	5.78	3.27
8	0.0041	6.12	2.51	1.01	0.0232	1.97	4.56	3.25
9	0.0044	4.11	1.81	0.89	0.0468	1.15	5.39	5.02
10	0.0099	1.47	1.45	1.20	0.0311	1.26	3.93	3.50
11	0.0212	0.55	1.16	1.57	0.0213	1.42	3.03	2.54
12	—		—	—	0.0478	0.77	3.71	4.21

The K_z values in midsummer 1979 (the only time interval studied in that year) were significantly lower than in all but two relatively windless time intervals studied in 1978. As in 1978, K_z was greater in the western basin. The low K_z values during the 1979 interval were a consequence of the abnormally low wind energy, high N_z^2 values in the upper thermocline, and high and increasing total water column stabilities accompanying above-normal air temperatures. Wind power averaged only 2.2 $\times 10^2\,J\cdot m^{-2}\cdot d^{-1}$ for the period, the lowest for any extended summer period investigated. The mixed layer temperatures averaged 2.5° above the July norm and were associated with midsummer bottom temperatures that were the lowest during the 9 yr the lake was studied (Table 2). Stability conditions during this time interval were thus more similar to those reported by Quay et al. (1980).

When we examine the pattern of K_z and N_z^2 vs depth there is no evidence of a depth trend in the western basin but a very pronounced lower metalimnetic K_z minimum in the eastern basin (Table 6). Although the minimum K_z values correspond to the maximum N_z^2 values, the relationship between the two parameters is not as simple as is frequently supposed (Quay et al. 1980; Jassby and Powell 1975). If K_z were inversely proportional to N_z^2, then the product of these parameters would be constant. As can be seen, the product decreases significantly and nearly monotonically in both lake basins and decreases more in the eastern than in the western basin. Furthermore, the product $N_z \times K_z$ shows a scatter but no depth trend in the western basin but is consistently low below 7 m in the sheltered eastern basin. The evidence from this time interval, and from other intervals as well, implies much reduced mixing intensities below 7 m in the eastern basin. This corresponds to wind sheltering and a short fetch length in the east basin for $z > 7$ m (Fig. 1).

Thermal Stratification during 1971–77

The highly individualistic time series for $\bar{h}_c^{max}(t)$ during the stratified periods in 1971–78 is illustrated in Fig. 6. Note that the midsummer thermocline depth is not typically 5 m, nor is the seasonal progression of the thermocline "consistent each year" as claimed by Larsen et al. (1979, 1981). Instead, a time series analysis of weather trends can account for the highly individualistic seasonal stratification in all of the years during which the lake has been intensively studied.

This is shown for 1971 by comparing appropriate panels in Fig. 3 and 6. A warm and nearly windless June followed a cool and windy late May. A shallow but late-arriving epilimnion was the result. Moreover, it overlay a relatively warm hypolimnion, as previously explained. High wind energy and a concomitant cooling trend caused the lake to turn over in late July 1971. The

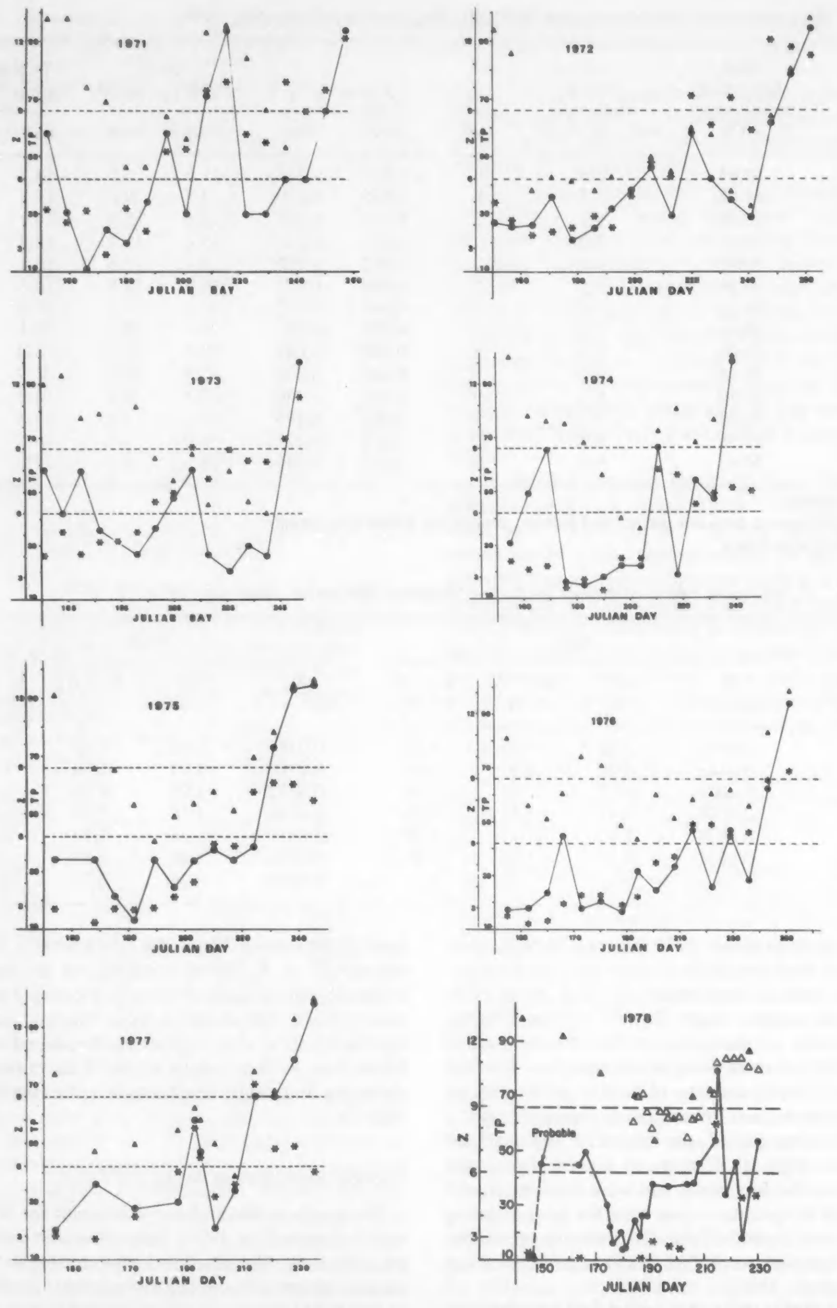

FIG. 6. Time series for basin-weighted maximum convective circulation depth (m), $\bar{h}_c^{\max}$(J.D.) (●), basin-weighted mean depth (m) of the 3 mg·L^{-1} dissolved oxygen isopleth at the deep holes, $\bar{R}_z$(J.D.) (▲), and basin-weighted mean mixed layer (above h_c in each basin) total P concentrations (mg·m^{-3}) (*). For 1978, $\bar{R}_z$(J.D.) (△) is based on conductance profiles. Parameter $\bar{h}_c^{\max}$(J.D.) estimated after subtracting 200–250 cal·cm^{-2} from upper portion of daytime temperature profiles.

lake restratified weakly and briefly during an interlude of warm weather in August.

The severe June cold front in 1974 caused a penetration of the mixed layer to a depth of 9 m (again compare Fig. 3 and 6). During the subsequent 38-d interval of low windpower and above-normal air temperatures the mixed layer was mostly shallow (~3 m). Then, the very powerful late July cold front caused the mixed layer to penetrate again to 9 m. Following a brief interlude, windy weather and below-normal air temperatures caused the complete turnover of the water column by late August.

By contrast, the deep penetration of the mixed layer in 1975 was delayed because of low wind energy until after day 218; this corresponded to the coupled effects of wind and a severe cooling trend in late summer.

The severe June cold front in 1976 caused a pronounced increase in mixed layer thickness, but $\bar{h}_c^{\max}(t)$ was less than during the corresponding power episode in June 1974. Unlike 1974, late May and early June were much warmer than normal in 1976; as a consequence, density stabilization was greater and the powerful wind event was less successful in deepening the mixed layer (also true of June 1972). The turnover progression following day 235 (in 1976) clearly resulted from the power and air temperature shift in late August of that year.

A sequence of cold fronts caused migration of the thermocline in early July 1977 after nearly 2 mo of low wind energy and a shallow mixed layer. As noted earlier, the hypolimnion was much warmer in June 1977 than in early summer 1972 because of the early ice-out in 1977. Because of the warmer bottom waters a severe cooling trend with only moderate wind energy lead to complete turnover before late August 1977. Conversely, the abnormally low bottom temperatures in 1972 (Table 2) prevented deep excursions of the thermocline in midsummer and prolonged the stratification into early September.

Station BPDH was sampled on 17 August 1967; the observed temperatures varied from 21.3°C at the surface to 18.1°C at 12 m (the deepest depth reported). From this the investigators concluded (Bradbury and Megard 1972, p. 2640) "A thermocline usually develops below depths of 3 to 4 m during mid summer, but the lake is so shallow that thermal stratification does not develop until water temperatures exceed 18 °C." Actually, it is more likely that the lake had been stratified for 2.5 mo and that this profile more nearly represented the terminal stage before "turnover." This quotation represents the "static" interpretation of summer thermal stratification as compared with the "dynamic" approach followed in this paper.

Water Column Redox and the Phosphorus Economy of the Mixed Layer

The progress of redox conditions below the mixed layer boundary and the lake-mean total P concentration in the mixed layer during each of the years of intensive study are shown in Fig. 6. As explained in Methods, sediments below the basin-weighted redox marker, $\bar{R}_z(t)$, have undergone the redox shift to anoxic conditions within the benthic boundary layer.

Close examination of Fig. 6 reveals important features of the redox and phosphorus cycles in this lake. First, the shift to anoxic sediment conditions below a depth of 7 m occurred at least once in each of the study years prior to 1978 and at least twice in each of five years. The onset and duration of such conditions were extremely variable and in accord with particulars of the individual weather series. Thus, neither anoxic conditions nor phosphorus concentrations in the mixed layer can be identified with fixed Julian day markings. This time dependency was assumed in the model of Larsen et al. (1979).

In 3 yr with unusually warm May weather and premature onset of stratification (1972, 1976, 1977) the sediment anoxic zone had ascended to 7 m prior to mid-June (compare Fig. 3 and 6). Two of these years were after the startup of the advanced waste treatment plant for the city of Ely. In contrast, relatively cold and windy June weather in 1978 interrupted the development of the hypolimnetic oxygen deficit.

The second and most important inference from Fig. 6 is that large increases in mixed layer total P occurred when the following two conditions jointly held. First, the antecedent zone of anoxia included an important fraction of the extensive metalimnetic sediments (6–10 m zone). Second, the mixed layer had migrated sharply downward in the most recent time interval and entrained metalimnetic water that had previously overlain anoxic metalimnetic sediments. There are numerous recorded examples of this phenomenon taking place as early as Julian day 195 (years 1971 and 1977, e.g. both before and after the profound alteration of the lake's external P loading).

In both 1971 and 1977 a long period of very low windpower and above-normal air temperatures was responsible for the stagnant mixed layer and the early anoxia and predated the subsequent phosphorus rise attending mixing. Notice also that the total P increases prior to Julian day 195 were virtually the same in 1971 and 1977 (a 100% increase in mixed layer total P) and attended identical penetrations of the mixed layer. In light of this it is important to stress an important time series difference between 1971 and 1977, namely that May weather was opposite in character in those two years. Thus, we can conclude that the total P increases were not simply a consequence of the duration of antecedent stratification. The special importance of this inference is stressed shortly.

Many of the correlations between total P increases and deep mixing are notably decisive, as evidenced by each week preceding Julian dates 195 and 208 (1971), 205, 220, and 247 (1972), 212 and 250 (1973), 211 (1974), 243 (1976), 193 and 214 (1977), and 215 (1978). The 1974 event is one of the most informative because deep mixing accompanied very high sustained windpower and followed mixed layer stagnation during 37 d of strongly above-normal air temperatures. The sediment anoxic zone ascended to 5 m during this low-power interlude immediately preceding the powerful July cold front. Clearly, any model of the phosphorus economy of the Shagawa mixed layer must be able to explain a 130% increase in total P in a single week and following seven trendless weeks.

In a few instances, $\bar{h}_c^{\max}(t)$ fails to shift during a time interval when the redox boundary has migrated sharply deeper and total P has surged in the mixed layer. The best example is the key interval following Julian day 218 in 1975. The redox boundary shifted deeper by more than 2 m during what proved to be the strongest cold front in summer 1975 (days 219–220) (cf. Fig. 3). No shift is apparent in $\bar{h}_c^{\max}(t)$ because the mixed layer boundary migrated upward again during the several days of low windpower following the cold front and preceding sampling. The mixed layer boundary at the end of the week interval was thus unrepresentative of the maximum value of the boundary during the week. This example also shows an important shortcoming of systematic lake sampling following a rigid sampling schedule. Stauffer (1980) showed that weekly intervals are close to the period of the cold front influences.

A significant downward migration of the 3 mg $O_2 \cdot L^{-1}$ isopleth can occur only if there has been accelerated eddy diffusion transport through the metalimnion in this lake. Water clarity in the mixed layer is too low to allow photosynthesis in the metalimnion; hence, in the absence of eddy diffusion transport of oxygen, the redox boundary is constrained to migrate upward. Downward translations of the redox boundary are thus more accurate indications of activated entrainment during some of the time intervals of interest. This is shown clearly by the extended Julian date period 188–230 in 1975. Although there is no decisive trend in $\bar{h}_c^{\max}(t)$ before day 225, during every interval when the redox boundary shifted to deeper water the total P concentration in the mixed layer increased. The weeks preceding both days 173 and 201 in 1976 are additional examples when the redox boundary moved to deeper depths and the total P concentration increased, but the mixed layer thickness showed a net decrease. The weather time series (Fig. 3) shows that on both occasions high wind energy preceded the terminating date by several days. The net decrease in $\bar{h}_c(t)$ occurred because of a shallower thermocline that became established during the windpower lull.

The long record of study proves that high wind energy and a rapid concomitant deepening of the mixed layer are not sufficient conditions to cause a significant increase in mixed layer total P concentration. This is shown by the June periods of high power in both 1974 and 1978. In contrast, the high windpower during June 1976 caused a doubling in total P concentration. Because of the very warm May and early June weather in 1976, anoxic conditions had set in early. The time series from several years also show that high windpower and thermocline migration in the late summer have little or no effect on mixed layer total P unless the immediately antecedent period featured low redox conditions above the metalimnion shelf sediments. This can be seen by contrasting 1971 conditions with those in 1974. Unlike 1971, the August interlude of warm, relatively calm weather was too short in 1974 to cause reestablishment of metalimnetic anoxia. A similar situation developed in 1978.

The time series for 1972, 1975, 1976, and 1977 show that once the mixed layer has penetrated to 10 m there is virtually no effect (on total P in the mixed layer) of its migrating on down to the bottom. The phosphorus economy of the mixed layer is controlled by events involving the middepth range (5–10 m) in the lake.

From the above time series analysis it is clear that increases in mixed layer total P concentration are neither a feature of the late summer nor are they directly relatable to the length of time the lake has been stratified. Thus, very large increases in total P occurred in both mid-July 1971 and July 1977. However, in 1971 the lake had been stratified for only 45 d. The period is short and out of phase compared with the life cycles of the macrophytes in the littoral zone. Finally, by showing that metalimnetic anoxia is a necessary condition for the phosphorus increase we have proved that the littoral zone sediments cannot be the source of the additional mixed layer phosphorus.

Conclusions

The transport of phosphorus into the mixed layer in Shagawa Lake is controlled by linkages among weather, lake morphometry, and in-lake biogeochemical processes. Explanation of the observed increases in total P in the mixed layer during the summer and the incomplete response of Shagawa Lake to an 80% reduction in external phosphorus loading requires an understanding of these linkages. From this investigation, the following conclusions can be reached.

1) The onset of thermal stratification is highly variable from year to year, depending on weather conditions. Warm, windless weather in May results in early stratification (late May). In contrast, cool, windy weather in May delays stratification until June. Variations in spring weather influence the lake's mixing regime during summer.

2) After the onset of thermal stratification, the convective circulation depth is highly variable within a given year and between years as determined by weather sequence and the shallowness of the lake. Stratification progresses separately in the two basins because of the longer wind fetch of the west basin.

3) The vertical eddy diffusivity in the main thermocline varies with depth, wind energy, basin exposure, and water column stability. during summer 1978, eddy diffusivities in the middle to upper portion of the thermocline ranged from 0.025 to $0.25\ \mathrm{cm}^2\cdot\mathrm{s}^{-1}$ in the west basin. These estimates are about one order of magnitude higher than arrived at by Larsen et al. (1981), based on Sweers' (1970) algorithm. Because of its shallowness, the assumptions underlying the use of Sweers' algorithm are violated for this lake during summer.

4) Large increases in total P in the mixed layer are a result of direct entrainment within the middepth zone. For large increases in total P to occur, two conditions must be satisfied. first, the anoxic zone below the mixed layer must include a large fraction of the middepth shelf (6–10 m) sediments. Subsequently, the mixed layer must migrate downward and directly entrain water overlying these anoxic shelf sediments. The large sediment area in the middepth zone of Shagawa Lake's west basin accounts for the importance of this process.

5) Littoral zone sediments and macrophytes cannot be the source of observed phosphorus increases in the mixed layer. Time series analysis shows that shelf-sediment anoxia is a necessary precondition for phosphorus increases. Furthermore, increases in mixed layer total P occur over short intervals that are out of phase with the growth or decomposition of macrophytes in the geographically restricted littoral zone.

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Babine Lake Sockeye Salmon (*Oncorhynchus nerka*) Enhancement Program: Testing some Major Assumptions

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McDonald, J., and J. M. Hume. 1984. Babine Lake sockeye salmon (*Oncorhynchus nerka*) enhancement program: testing some major assumptions. Can. J. Fish. Aquat. Sci. 41: 70–92.

The objective of the Babine Lake sockeye salmon (*Oncorhynchus nerka*) enhancement project was to increase fry outputs (and thus, smolt outputs and adult returns) by expanding and improving available spawning beds through the use of artificial spawning channels and related water flow control facilities. The project proceeded on four basic assumptions: (1) the artificial spawning channels would prove an effective means of producing sockeye fry, (2) the fry produced would be as viable as those produced from natural spawning beds, (3) the lake nursery area had the capacity to support larger juvenile populations, and (4) increased smolt outputs would result in increased adult returns. A before and after study has allowed these assumptions to be tested. Egg-to-fry survival in the channels was close to 40%, as expected. Comparisons of wild and channel-produced fry did not reveal any substantial difference in their distribution, growth, and survival in the lake. Increases in the abundance of fry were followed by corresponding increases in the abundance of underyearlings in the lake and seaward migrating smolts. No significant change in the average size of the juveniles or their survival in the lake could be detected when population size increased. While the assumptions regarding juvenile production were found to be generally valid, adult returns did not meet expectations. This was due largely to the lack of response to increased smolt outputs from even-numbered brood years. Some options for future management are offered.

Le projet de mise en valeur du saumon nerka (*Oncorhynchus nerka*) du lac Babine avait pour objectif une production accrue d'alevins (et, partant, de smolts et de retours d'adultes) en élargissant et améliorant les frayères accessibles par le biais de chenaux de ponte artificiels et de diverses installations de contrôle du débit de l'eau. Le projet reposait sur quatre hypothèses fondamentales: (1) les chenaux de ponte artificiels sont un moyen efficace de produire des alevins de saumons, (2) les alevins produits sont aussi viables que ceux provenant de frayères naturelles, (3) la région d'alevinage du lac peut supporter de plus grandes populations de juvéniles et (4) une production accrue de smolts résulte en un plus grand nombre de retours d'adultes. On a pu vérifier ces hypothèses, grâce à des études menées avant et après la mise en œuvre du projet. La survie, de l'œuf à l'alevin, dans les chenaux se rapproche de 40%, tel qu'anticipé. Des comparaisons d'alevins produits dans la nature ou dans les chenaux n'indiquent pas de différence substantielle de leur distribution, croissance et survie dans le lac. Les augmentations du nombre d'alevins sont suivies d'augmentations correspondantes des poissons de moins d'un an dans le lac et de smolts émigrant vers la mer. L'augmentation de taille de la population ne semble pas être accompagnée de changement significatif de la taille moyenne des jeunes ou de leur survie dans le lac. Si les hypothèses touchant la production de juvéniles sont généralement valides, les retours d'adultes sont inférieurs à ce que l'on avait anticipé. Ceci est dû en grande partie au fait qu'une production accrue de smolts d'années paires n'a pas eu d'effet. Certaines options pour la gestion future sont sont offertes.

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The Skeena River system is one of the major sockeye salmon (*Oncorhynchus nerka*) producers in British Columbia. Over the past 30 yr the average production of adult sockeye (catch plus spawning escapement) has been about 1.5 million annually. While numerous lakes in the drainage contribute to sockeye production, by far the largest and most important of these is the Babine Lake system, which contributes 90% or more of the total (Larkin and McDonald 1968).

Johnson (1956, 1958, 1961), after examining the distribution, abundance, and growth of juvenile sockeye in the various Babine Lake basins, concluded that the Main Lake basin was underutilized as a nursery area because of the limited capacity of adjacent spawning grounds to accommodate the number of spawning adults required to produce sufficient fry. This work led to an enhancement project (Anonymous 1965, 1968) aimed at increasing the number of fry entering the Main Lake. Three artificial spawning channels were built, two adjacent to the Fulton River and the third adjacent to Pinkut Creek (Fig. 1). The channels provided an additional 117 000 m^2 of spawning area expected to accommodate 220 000 spawners and produce an additional 125 million fry. In addition, water flow control structures were built at both locations to serve the spawning channels and to regulate river discharges with the expectation of increasing fry production in the existing natural spawning beds. The first spawning channel on Fulton River became operative in

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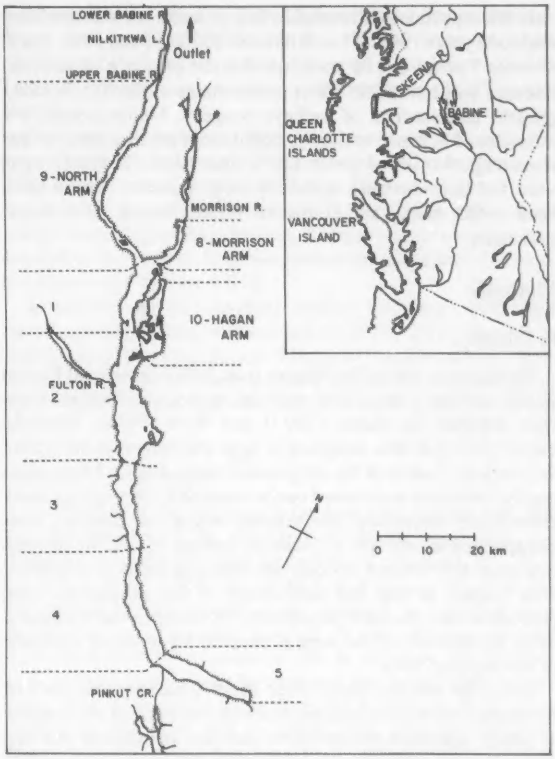

FIG. 1. Babine Lake system showing fishing areas.

1965. Flow control began on Fulton River and Pinkut Creek in 1968. Also, in this year the Pinkut Creek channel became operative. The first stage of Fulton channel No. 2 was completed in 1969. By 1971 all channels were fully operational.

The enhancement project proceeded on a number of important assumptions: (1) artificial spawning channels would prove to be an effective means of producing sockeye fry, and an egg-to-fry survival rate of 40% (at least double the observed rate from natural spawning beds) was anticipated as was an output of 125 million fry, (2) the viability of the fry produced would be comparable with that of fry produced naturally, (3) the Main Lake nursery area had the capacity to support the much larger juvenile population, and (4) an increase in the juvenile output from the lake would result in a corresponding increase in the number of returning adults. A catch of an additional 1 million adult sockeye was projected.

Monitoring the sockeye population at various life history stages before and after the enhancement project came "on-stream," provided an opportunity to examine these assumptions. Data on parent spawners and fry outputs are available from Ginetz (1977) and West (1978). Comparisons of the distribution, growth, and survival of channel-produced fry and wild life fry from natural spawning beds were made by McDonald (1969). Additional work hereto unpublished provides further comparisons and data bearing on the question of lake nursery area capacity. Finally, estimates of the annual number of seaward migrants and resulting adult returns are available to examine differences in sockeye production in pre- and post-enhancement years.

This paper has been organized to address each of the four assumptions more or less in the order given above. Specifically, we will examine the following: (1) evidence of change in annual fry outputs as a result of the artificial spawning channels and subsequent changes in the abundance of underyearlings and seaward migrants, (2) comparisons of the distribution, growth, and survival in the lake of distinctively marked wild fry (from natural spawning grounds) and channel-produced fry to test the assumption of equal viability, (3) evidence of the dispersal and subsequent distribution of fry and juveniles in the lake to determine the extent to which the available lake nursery area is utilized, (4) the effects of increased population size and density on the size and growth of fry, to the seaward migrant stage, and (5) change in the abundance and age composition of returning adults in response to increased outputs of seaward migrants.

Background

Babine Lake, part of the Skeena River drainage, is one of the largest in British Columbia (Fig. 1). It is 150 km long and up to 7 km wide. This lake, together with the small and connecting Nilkitkwa Lake, provides about 500 km^2 of sockeye nursery area. The various lake basins are characterized as follows:

	Surface area (km^2)	Maximum depth (m)	Mean depth (m)
Main Lake	400.8	186	62.5
North Arm	54.4	46	20.1
Morrison Arm	17.7	31	11.4
Hagan Arm	17.7	83	28.4
Nilkitkwa Lake	4.9	21	7.8

Details of the Babine Lake system's physical and chemical characteristics are provided by Johnson (1965a, 1965b), Narver and Anderson (1969), Stephens et al. (1969), McDonald and Scarsbrook (1969), and Stockner and Shortreed (1976).

Sockeye spawn mainly in September and October. The resultant fry emerge from the gravel the following spring (May and June) and migrate into the lake. Most remain in the lake 1 yr (underyearlings) then migrate to sea (smolts). A small percentage (<2%) spend 2 yr in the lake before seaward migration. Most return as maturing adults after spending 2 or 3 yr at sea.

Each year since 1946, sockeye returning to Babine Lake have been counted through a fence located on the Babine River, downstream of the spawning beds (Aro 1961; West 1978). Their numbers have ranged from 102 000 to 888 000 annually and averaged 668 000. Spawning takes place in all accessible streams but major spawnings occur in the upper and lower Babine River, Fulton and Morrison rivers, and Pinkut Creek. Spawning ground estimates for 1949–77 (West 1978) reveal that on average, 52% of the sockeye spawn in streams adjacent to the Main Lake, 44% in the Babine River adjacent to the North Arm, and 4% in Morrison Arm. Hagan Arm is devoid of adjacent spawning streams.

Some additional spawning has been observed to occur along the Main Lake shore but no quantitative information is available. Observed differences between annual fence counts and estimates of the number of spawners in the tributary streams suggest that up to 20% of the sockeye entering Babine may spawn in the lake.

Distribution of Underyearlings

Past studies have revealed some important features of the distribution and behavior of juvenile sockeye in the lake. Johnson (1956, 1958, 1961, 1965b) concluded that dispersal of fry from their natal streams was limited and this, together with the multibasin nature of the lake, resulted in distinct populations in more or less distinct basins. His comparisons of population densities, food supply, and size of underyearlings among lake basins led him to propose that at high densities food became limited, growth was slowed, and compensatory mortality occurred.

However, McDonald (1969) found that in the Main Lake at least, distribution was not static but changed continuously through summer and fall. Fulton River fry dispersed rapidly into the lake, some as far as 71 km from the river by early July. Initially, underyearlings were found concentrated in the southern half of the Main Lake. As the season progressed the population shifted into central and northern areas.

McCart (1967) observed that in the North Arm as well as in the Main Lake, fry may disperse considerable distances from their natal stream. Fry from the Babine River were observed moving in schools along the shores of the North Arm as far as 32 km uplake, the most distant point of McCart's observations.

Whether underyearling distribution is more or less static, as described by Johnson, or dynamic, as described by McDonald and McCart, bears importantly on the question of lake nursery area capacity and the mechanisms that may determine it. Pertinent new information will be examined in this report to elucidate this question.

Kokanee

Kokanee, the nonanadromous form of *O. nerka*, are present in Babine Lake. They spawn, usually in their 4th yr, in most tributaries but most abundantly in small streams adjacent to the Main Lake. The abundance of spawners has varied greatly. Johnson (1958) cited reports of over 1 million spawners in 1955 and 1956, and H. W. D. Smith (Fisheries and Oceans, Vancouver, B.C., personal communication) observed about the same number in 1963. McCart (1970), after almost complete coverage of kokanee spawning streams from 1964 to 1967, estimated an average of 40 800 spawners per year (range 18 000–64 000). Comparable coverage by H. W. D. Smith in 1968 (personal communication) and by J. McDonald in 1969, 1970, and 1972 (unpublished data) revealed an average of 32 500 (range 26 000–35 000).

Mature kokanee are readily distinguished from sockeye by their relatively small size. However, no satisfactory way has been found to distinguish between juveniles of the two types. Although kokanee eggs and the resulting fry are smaller on average than those of sockeye (McCart 1970), the difference is not great enough to separate the two types subsequently in a mixed population of juveniles.

Johnson (1958) compared the potential egg depositions of kokanee and sockeye in the 1955 and 1956 brood years and estimated that as much as 70 and 39% of the ensuing juveniles in the Main lake could be the progeny of kokanee. The much smaller kokanee spawning populations in more recent years would reduce the proportions of juvenile kokanee accordingly. Comparisons of potential egg deposition of the two types for the 8 yr between 1964 and 1972, for which data are available, suggest that from 1 to 3% of the ensuing underyearlings in the Main Lake would be the progeny of kokanee.

In this report, we will compare lake juvenile populations from the brood years 1965–67 with those of 1970–72 and 1976. For 5 of those 7 yr we can be confident that the presence of juvenile kokanee will have little effect on estimates of the distribution, growth, and survival of sockeye progeny. Unfortunately, no estimates of kokanee spawning populations are available for the remaining two brood years (1971 and 1976). Probably they were not large because unusually large numbers would have been noted during the course of annual counts of sockeye spawners.

Methods

Fry Outputs

Estimates of annual fry outputs from Fulton River and Pinkut Creek and their associated artificial spawning channels have been reported by Ginetz (1977) and West (1978). Methods varied from hydraulic sampling of eggs and alevins in the gravel to complete counts of fry migrants (Ginetz 1977). Most commonly, estimates were based on the catch of fry in traps operated periodically throughout downstream migration. Catches were extrapolated to take into account the volume of river or channel discharge not flowing through the traps and times of operation with respect to the diel periodicity of the migration. This procedure was checked periodically by independent estimates based on recovery in the traps of marked fry released upstream of the trapping sites.

Since fry outputs from other Main Lake streams are not monitored, we have estimated them on the basis of the number of parent spawners (West 1978) and the assumption that fry output per spawner was equal to the average estimated from natural spawning in the Fulton River and Pinkut Creek (233 fry per spawner). These estimates are gross, but when added to the much larger outputs recorded from Fulton River and Pinkut Creek and their spawning channels, the resulting totals are considered to provide useful estimates of the numbers of fry entering the Main Lake. These estimates, however, do not include fry that may have resulted from the unknown number of sockeye that spawn in the lake rather than in its tributaries. As a result, our estimates of Main Lake fry populations are probably conservative.

Lake Resident Juveniles (Underyearlings)

Underyearlings were captured from early summer through fall using a 10.7 m vessel equipped with a purse seine. The net was half-purse, 274.4 m long, with an effective fishing depth of 15.7 m. Mesh size varied from 0.48 cm in the bunt to 3.81 cm in the lead. details of the equipment and procedure are provided by Scarsbrook and McDonald (1970).

Seining was carried out in 1966–68, 1971–73, and again in 1977 in eight lake areas, which generally coincided with natural lake basins and prominent land features (Fig. 1). In 1966, set (fishing) locations were not predetermined but were distributed as widely throughout the lake as time and effort permitted. By using a map grid, set locations were randomly determined (Scarsbrook and McDonald 1970) in 1967, with the proviso that areas 1–5 and 9 would have 10 locations and areas 8 and 10 would have 5 locations each. The same set locations were used in subsequent years.

Seining was carried out routinely during three fishing periods each year: session I in late June and early July, session II in late August and early September, and session III in early October.

Each session was usually of 10–15 d duration. Since underyearlings were only available in the surface layer at night (McDonald 1969, 1973), seining was confined to hours between times of evening and morning civil twilights for 55° north latitude.

Captured fish were recorded by species and samples were taken for length and weight measurements. After hardening in 10% formalin until stabilized (Parker 1963), fork length was measured to the nearest millimetre. From 1966 to 1968, mean weight was calculated by dividing the total sample weight by the number in the sample. In subsequent years, individual fish were weighed to the nearest 0.01 g.

In addition to the standard netting procedures described above, special seining was carried out on several occasions to provide ancillary information. Catches of underyearlings from these nonstandard sets have not been used in this analysis except for a number of marked fish, which were included in growth analysis.

Marking and Recovery

Two marking and recovery programs were carried out. The first involved fry from the 1965–67 brood years and was designed to compare wild and channel-produced fry. In a second program (1970 and 1971 brood years), fry from the Fulton and Pinkut systems were marked to compare their distribution, growth, and survival in the lake at pre- and post-enhancement population levels. In all cases, fry migrants were marked distinctively by excising one or the other or both pelvic fins. Recoveries were made by examining purse-seine catches in the lake and by examining seaward migrants. Methods and resulting data have been reported by Scarsbrook and McDonald (1970, 1972) and Coburn and McDonald (1972, 1973). Analysis of results of the 1965 brood year program was reported by McDonald (1969).

One of the assumptions upon which the marking programs were based was that the incidence of naturally missing fins was zero or at least not large enough to compromise comparison of the marked stocks. For the 1965–67 comparisons of wild and channel fry, right (wild) and left (channel) pelvic marks were used. Fry for the 1970 and 1971 broods were marked with the right pelvinc (Pinkut Creek), left and double pelvic (Fulton River, 1970), and double pelvic only (Fulton River, 1971).

McDonald (1969) examined 3104 fry migrants from the unmarked 1965 brood and 4200 smolts from the unmarked 1964 brood without finding any missing pelvic fins. Another examination of 4650 smolts from the 1968 brood gave the same result. An extensive test of the incidence of natural marks was carried out on underyearlings of the 1972 brood. None of the fry of that brood year were marked. Examination of 81 733 underyearlings captured by purse seining in the lake resulted in 32 fish found with one or both pelvic fins missing. The numbers and types of natural "marks" found were as follows:

Type	No.	Marked: unmarked ratio
Right pelvic	13	1:6287
Left pelvic	16	1:5108
Double pelvic	3	1:27244
All	32	1:2554

The cause of the missing fins is unknown but deformities are a possibility as is fin loss from bacterial infection (fin rot). Whatever the cause, it did not appear to discriminate between one fin or the other. The incidence of missing right and left pelvic fins was not significantly different ($\chi^2 = 0.310$, $P = 0.60$). The incidence of both pelvics missing was very low; presumably the chances of a fish losing the pair of fins were much less than those of losing only one.

The incidence of natural marks in the 1972 brood underyearlings was greater than that anticipated from the earlier but much smaller tests. However, while bothersome, the incidence is still very low and the presence of natural marks would make up a very small fraction of mark recoveries in years in which marking programs were carried out. For example, during the 5 yr of surveys, a total of 1284 marked fish were found among 205 120 underyearlings examined. Assuming that the 1972 brood incidence of naturally missing fins applied to all years (1:2554) then their estimated number in the 1284 marked fish would be 80, or 6%, of the total. The resulting error in interpretation of the marking and recovery data would be very small. Since the incidence of naturally missing right and left pelvic fins appears to be the same, comparisons of marked wild and channel fry would remain valid. However, estimates of survival rates of marked fry would be somewhat greater than the actual rates. The existence of natural marks demands caution when describing distribution of marked stocks, particularly in those lake areas where the marked to unmarked ratio was extremely low.

Seaward Migrants

The number of smolts migrating from Babine Lake has been estimated on a daily and seasonal basis for over 20 yr. Each day of the migration, smolts were tagged and released into the migrant population passing through Nilkitkwa Lake. Smolts captured in a trap about 5 km downstream were examined for tags (Jordan and Smith 1968). Procedures for estimating population size from the tag and recovery data are given by McDonald and Smith (1980).

This seaward migration is typically bimodal, with "early run" smolts originating from the North Arm and "late run" smolts from the Main Lake basin (Johnson and Groot 1963; McDonald 1969; McDonald and Smith 1980). The bimodality of the migration, together with differences in size between early and late smolts plus some behavioral changes noted by H. W. D. Smith (personal communication), has allowed separate estimates of smolt outputs from the North Arm and Main Lake. Estimates used in this report are from unpublished Department of Fisheries and Oceans files.

Returning Adults

Records of the annual catch and escapement of Skeena sockeye are kept by staff of the Department of Fisheries and Oceans. In addition, routine sampling and scale analysis is carried out to determine the age composition of each year's run so that adult returns can be related to brood year escapements. Available information does not allow a separate estimate of returns to Babine Lake, but since the Babine stock makes up more than 90% of the total, returns to the Skeena as a whole will provide close approximations.

Analysis

The number of years of observation required to examine changes in sockeye production before and after enhancement resulted in a large volume of data. To reduce the amount of

TABLE 1. Abundance of Main Lake juvenile sockeye at various life history stages (*$P = 0.05$; **$P = 0.01$; ***$P = 0.001$; NS, not significant).

Brood year	Pinkut and Fulton fry (millions)	Total fry (millions)	Underyearlings Session I, July (lake index)	Session II, August (lake index)	Session III, October (lake index)	Main lake smolts (millions)	Survival fry–smolts (%)
1961	36.8	77.4				5.78	7.5
1962	46.7	72.1				29.35	40.7
1963	57.5	89.7				19.16	21.4
1964	29.0	47.0				13.78	29.3
1965	31.5	38.2	80.8	76.3	28.7	6.84	17.9
1966	53.2	61.2	102.7	84.3	29.5	18.10	29.6
1967	47.5	64.9	132.3	146.3	20.7	24.18	37.3
1968	75.7	98.4				34.63	37.2
1969	59.5	78.6				39.20	49.9
1970	114.9	134.7	167.1	193.1	113.9	44.56	33.1
1971	152.1	161.2	385.4	297.9	82.8	73.98	45.9
1972	158.5	170.6	328.6	198.9	106.7	61.13	35.8
1973	150.7	183.2				27.43	15.0
1974	107.0	134.9				36.12	26.8
1975	158.3	174.6				51.01	29.2
1976	228.8	232.5	340.5	212.7	150.6	70.92	30.5
1961–67							
Mean	43.2	64.4	105.3	102.5	26.3	16.7	26.2
SD	10.91	17.64	25.85	39.20	4.87	8.66	11.52
1970–76							
Mean	152.9	170.2	305.4	225.6	113.5	52.2	30.9
SD	39.53	33.31	95.39	48.86	28.10	17.50	9.37
t-test	7.079***	7.432***	3.463*	3.592*	5.198**	4.802***	0.83 (NS)

tabular material in the text, statistical analysis of underyearling density and abundance derived from catch per unit effort data and analysis of size data are presented in the appendix.

Comparison of pre- and post-channel fry and smolt production has been based on two series of brood years: 1961–67 and 1970–76. Although a small artificial spawning channel on Fulton River (channel No. 1) was operative in 1965–67, the number of fry produced did not appreciably change the total fry outputs into the Main Lake from those of previous years, and for our purposes 1965–67 has been considered representative of the preenhancement period. The years 1968 and 1969 were years of transition, with the Pinkut Creek channel operative in 1968 and the first stage of a second Fulton River channel operative in 1969. These 2 yr have been excluded from our comparisons. The spawning channels began to approach designed production in 1970.

Results

Change in Abundance

Fry production from the artificial spawning channels was close to the 40% projected. Data from West (1978) showed that the average egg-to-fry survival in Fulton channel No. 1 was 48.7% ($N = 11$ yr), 43.4% in Fulton channel No. 2 ($N = 8$ yr), and 30.1% in the Pinkut Channel ($N = 8$ yr). However, flow control over the natural spawning grounds in Fulton River or Pinkut Creek did not result in increased production. West (1978) reported pre- and post-flow control average egg-to-fry survivals at Fulton River of 20.8% ($N = 7$ yr) and 17.2% ($N = 9$ yr), respectively. The means are not significantly different ($t = 1.23$, $P > 0.20$). Similarly, means of 11.1% ($N = 5$ yr) and 14.9% ($N = 9$ yr) at Pinkut Creek were not significantly different ($t = 1.23$ $P > 0.20$).

As a result of channel production, there occurred a large increase in fry outputs from the two systems as channels were brought to full operation (Table 1). Average annual outputs increased significantly from 43.2 million (1961–67) to 152.9 million (1970–76), an increase of 3.5 times ($t = 7.079$, $P < 0.001$). For the Main Lake as a whole the increase was less, nearly threefold (means 64.4 million and 170.2 million, $t = 7.432$, $P < 0.001$).

Greater fry outputs were followed by larger Main Lake underyearling populations. The lake population index (see Appendix) in sessions I and II increased between two- and three-fold, while in session III, the increase was more than four times the earlier level (Table 1). All differences in pre- and post-enhancement means were significant ($P \leqslant 0.05$).

Average Main Lake smolt outputs increased more or less proportionately from 16.7 million to 52.2 million, a threefold increase ($t = 4.802$, $P = 0.001$). The increase for Babine System as a whole (i.e. including smolt production in the North Arm) was somewhat less, 30.1 million to 68.2 million (Table 12), an increase of 2.3 times.

Validity of Abundance Estimates

Because error limits are not available for the individual estimates of juvenile abundance, we have examined the relationships between the estimates at successive life history

TABLE 2. Relationship of abundance estimates of sockeye from one sampling period with estimates at later time periods.

Life history stage				
X	Y	Linear regression	P ($b = 0$)	r^2
Fry migrant	Session I	$Y = 43.653 + 1.566X$	<0.01	0.79
	Session II	$Y = 81.593 + 0.812X$	<0.05	0.58
	Session III	$Y = 2.579 + 0.655X$	<0.01	0.87
	Smolts	$Y = 6.278 + 0.302X$	<0.01	0.74
Session I	Session II	$Y = 52.453 + 0.548X$	<0.01	0.81
	Session III	$Y = 12.252 + 0.290X$	NS	0.53
	Smolts	$Y = -2.284 + 0.205X$	<0.01	0.94
Session II	Session III	$Y = 1.803 + 0.430X$	NS	0.43
	Smolts	$Y = -13.092 + 0.323X$	<0.01	0.87
Session III	Smolts	$Y = 9.214 + 0.441X$	<0.05	0.69

stages given in Table 1. Evidence of a good relationship would support their validity whereas the absence of such a relationship would indicate that one or more of the estimates were very much in error or that annual variability in survival between life history stages was large.

Initially, two sets of regressions were calculated, one using the combined fry outputs from Fulton River and Pinkut Creek, the other using estimates of the total fry input to the Main Lake. No significant differences were found in the slopes of the two regressions. Because Fulton River and Pinkut Creek fry estimates are the most accurate and since the fry outputs from these streams make up most of the Main Lake total, regressions based on Fulton River and Pinkut Creek outputs only are presented here (Table 2).

All relationships were positive and in all but two, slopes were significantly greater than zero. If we ignore the two exceptions for the moment, the coefficients of determination (r^2) fell between 0.58 and 0.94, indicating a close relationship between the abundance estimates at successive life history stages. Both exceptions involved the abundance index for session III, suggesting that the estimates derived in October may be more unreliable than the others.

Survival Rates

Total juvenile populations

Based on estimates of total fry outputs into the Main Lake basin and resulting smolt outputs, survival rates ranged from 7.5 to 49.9% (Table 1). Average annual rates for the pre- and post-channel periods of 26.2 and 30.9 %, respectively, were not significantly different ($P > 0.40$).

Marked populations

The fry marking and recovery programs carried out over five brood years (Tables 3 and 4) provided opportunities for comparing wild and channel-produced fish (1965–67 brood years) and comparing survival rates in pre- and post-channel periods (1965–67 and 1970 and 1971 brood years). Also, survival rates for the marked populations could be compared with those derived from estimates of total fry output and smolt outputs from the Main Lake to test the validity of the two sets of estimates.

The relative survival of marked wild and channel fry was determined by comparing the marked ratio at time of release with those observed in underyearlings captured in the lake (sessions I–III) and finally among seaward migrating smolts (Table 3, 1965–67). The marked ratios found among the underyearlings varied considerably each year (due at least in part to the small number of recoveries in some instances), but no significant differences from the ratios at times of release were found when tested by chi-square ($P = 0.05$).

Comparisons of the ratios of marked seaward migrants given below are values for total, pooled, and heterogeneity chi-square (Sokal and Rohlf 1969) based on the numbers of marked wild and channel smolts observed daily throughout each annual migration:

Brood year	χ^2	df	P
1965			
Total	26.67	14	0.025
Pooled	2.61	1	0.090
Heterogeneity	24.06	13	0.030
1966			
Total	37.24	26	0.080
Pooled	13.25	1	0.005
Heterogeneity	23.99	25	0.500
1967			
Total	62.18	34	0.005
Pooled	23.71	1	0.005
Heterogeneity	38.47	33	0.250

Values of total chi-square were significant in 2 yr (1965 and 1967) and approached significance in the third, revealing day-to-day deviations from the expected ratio of wild and channel smolts during their migration. The significant pooled chi-squares in 1966 and 1967 indicate that the deviations were strongly in one direction. This was confirmed by the nonsignificant values of heterogeneity chi-square in those years. Thus, there were fewer than expected channel-produced smolts from the 1966 brood year and just the reverse from the 1967 brood. In 1965, pooled chi-square, while falling short of significance, suggests a tendency for fewer than expected wild smolts. However, the significant heterogeneity chi-square reveals that during the migration there were deviations from the expected ratio in both directions.

The above differences would, of course, be reflected in differences in the absolute survival rates of the two marked groups. Estimates of these survival rates can be made, since the number of marked fry released is known and the total number of marked smolts each year can be estimated by applying daily marked to unmarked ratios with daily estimates of smolt abundance and summing for the period of smolt migration (see Table 2 in McDonald 1969 for details of this procedure for 1965 brood year smolts). Survival rates are compared below (rates for the 1970 and 1971 brood years are included as a convenience for later discussion of pre- and post-channel periods):

Brood year	Group	No. marked and released	Estimated No. in smolt run	% survival
1965	Wild	203 754	25 895	12.7
	Fulton channel No. 1	299 363	42 848	14.3
1966	Wild	223 860	57 803	25.8
	Fulton channel No. 1	429 364	85 393	19.9
1967	Wild	325 727	95 308	29.3
	Fulton channel No. 1	341 607	113 367	33.2
1970	Fulton channel No. 2	366 661	91 503	25.0
	Pinkut channel	308 779	73 917	23.9
1971	Fulton channel No. 2	1 168 184	434 585	37.2
	Pinkut channel	550 062	140 623	25.6

TABLE 3. Marking and recovery of wild and channel fry, 1965–67 brood years.

				No. recovered							
	No. marked and released			Session I		Session II		Session III		Smolts	
Brood year	Wild	Channel	Lake area	Wild	Channel	Wild	Channel	Wild	Channel	Wild	Channel
1965	203 754	299 363	1	0	0	4	4	0	0		
			2	10	29	18	24	12	16		
			3	10	22	13	27	2	3		
			4	14	9	15	18	4	3		
			5	1	2	2	2	1	0		
Total				35	62	52	75	19	22	487	790
Marked ratios	0.405	0.595		0.361	0.639	0.409	0.591	0.463	0.537	0.381	0.619
1966	223 860	429 364	1	0	0	1	2	0	4		
			2	1	1	1	6	1	1		
			3	3	7	1	8	0	7		
			4	11	17	8	8	2	2		
			5	2	2	1	2	3	2		
Total				17	27	12	26	6	16	754	1222
Marked ratios	0.343	0.657		0.386	0.614	0.316	0.684	0.273	0.727	0.382	0.618
1967	325 727	341 607	1	1	0	8	6	0	2		
			2	0	3	10	10	1	1		
			3	18	22	2	4	1	5		
			4	23	37	18	15	2	0		
			5	14	8	6	2	1	0		
Total				56	70	44	37	5	8	1228	1551
Marked ratios	0.488	0.512		0.444	0.556	0.543	0.457	0.385	0.615	0.442	0.558

TABLE 4. Marking and recovery of fry from the Fulton and Pinkut channels, 1970 and 1971.

Brood year	Fulton channel No. 2	Pinkut channel	Lake area	Fulton	Pinkut	Fulton	Pinkut	Fulton	Pinkut	Fulton	Pinkut
1970	366 661	308 779	1	0	0	7	2	1	0		
			2	2	0	11	5	3	3		
			3	7	1	3	8	5	6		
			4	8	0	8	9	4	9		
			5	13	16	1	1	6	1		
Total				30	17	30	25	19	19	726	571
Marked ratios	0.543	0.457		0.638	0.362	0.545	0.455	0.500	0.500	0.560	0.440
1971	1 168 184	550 062	1	1	0	34	7	29	12		
			2	21	1	26	12	4	7		
			3	30	2	10	5	2	1		
			4	42	13	25	16	3	3		
			5	102	45	20	11	10	9		
Total				196	61	115	51	48	32	2214	683
Marked ratios	0.680	0.320		0.763	0.237	0.693	0.307	0.600	0.400	0.764	0.236

Annual rates for the 1965–67 brood years varied just over twofold for each group: from 12.7 to 29.3% and from 14.3 to 33.7% for wild and channel fry, respectively. However, the year-to-year change in the rate of one group was closely paralleled by that of the other, and when rates within years are compared they are similar. Clearly, the differences found by comparing marked ratios were too small to cause much difference in percent fry-to-smolt survival. In view of the small differences observed and the fact that they went both ways (a survival advantage for channel fry in 2 yr and for wild fry in 1 yr), we concluded that wild and channel-produced fry were similarly viable.

The fry-to-smolt survival rates of marked fish provide a second opportunity to compare rates for the pre- and post-channel periods, although the small number of brood years (5) for which information is available precludes meaningful statistical testing. Survival rates in the postchannel years of 1970 and 1971 were comparable with those in two prechannel years and greater than the rates in the third, supporting the conclusion arrived at using survival rates from total fry and smolt outputs, i.e. that there were no differences in survival between pre- and post-channel periods.

Validity of survival rates

The survival rates of marked fish and those of the total population were estimated independently of each other. The extent to which the two sets of estimates agree will provide a measure of their validity. Since there are two estimates for marked fry in each brood year (fry from two sources), it had to be decided which of the two (or the mean) should be used. It was decided that the rates from the source that produced the largest number of fry would be most representative. Data from West (1978) showed that by far the largest single source of fry was the Fulton River from 1965 to 1967 and Fulton channel No. 2 from 1970 and 1971. Regression analysis was carried out on the following pairs of survival rates:

	1965	1966	1967	1970	1971
Marked fry	12.7	25.8	29.3	25.0	37.2
Total fry	17.9	29.6	37.3	33.1	45.9

A high degree of association was found ($r^2 = 0.973$) when the estimates from marked fry were regressed on those derived from total fry and smolt outputs. A simple inspection of the paired values reveals that the rates for marked fish were consistently low by 4–9 percentage points. This is not surprising because some marking mortality could be expected. It is most likely that the higher rates estimated from total fry and smolt outputs are the more accurate.

Underyearling Distribution in the Main Lake

Total population

Distribution in terms of both density and abundance was examined for each fishing period using two-way analysis of variance with years and lake areas as treatment factors (Table A1). Estimates of relative density were derived from catch per unit of effort data (average catch per set) in each area, while estimates of relative abundance were calculated by weighting catches by area size as described in the appendix.

Looking first at densities in session I, significant differences were found among years and among lake areas within each year. However, the interaction term was not significant, showing that densities were distributed among the five lake areas in a similar way each year (i.e. no change before and after spawning channel operation). In sessions II and III, densities among years were again significantly different but differences among areas were significant only in session II. The significant interaction factor show that in contrast with session I, differences among areas varied from year to year.

Area densities were compared using Duncan's multiple range test modified for samples of unequal size (Table A2). During session I, in both pre- and post-channel years, there was a consistent increase in underyearling density from area 1 at the north end of the Main Lake to either area 4 or 5 in the south. In subsequent periods the north–south gradient was no longer apparent and no consistent pattern in distribution can be seen except in session II when the density in area 4 was either the greatest or second greatest. When pre- and post-channel years are compared, there is no evidence of a persistent change in distribution.

Distribution in terms of abundance was generally similar to that for density, revealing that differences in area densities were large enough to mask most of the effects of differences in area size. Significant differences in area indices occurred among years and among areas in all three fishing periods (Table A1). Again, the interaction terms demonstrate that distribution was consistent over the years during session I but variable in sessions II and III. When comparing area indices in session I (Table A3), there was consistently fewer underyearlings in area 1 and greatest numbers usually in area 4 or 5. Later in the season, distribution was more variable although usually underyearlings were most abundant in areas 2 and 4.

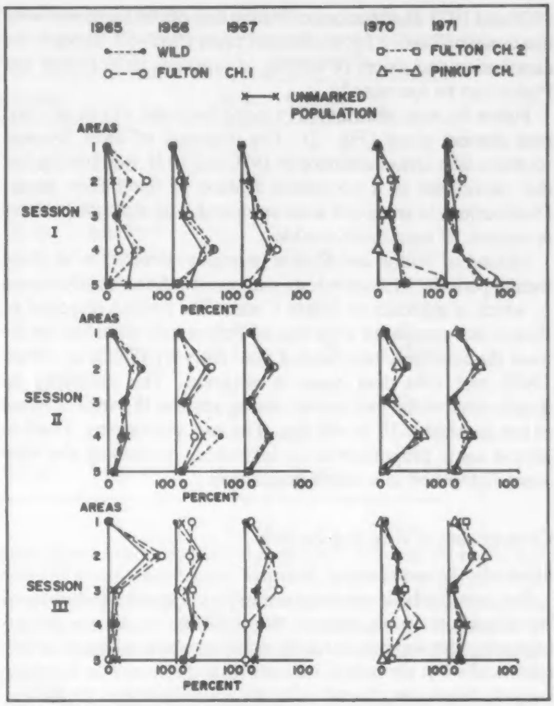

FIG. 2. Proportions of marked and unmarked underyearling sockeye in Main Lake areas by brood year and fishing period.

Marked underyearlings

The proportions of marked fish in Main Lake areas were estimated by applying the marked to unmarked ratio observed in each area to the area index of abundance drawn from Table A3 (for an example of detailed calculations see those for the 1965 brood year in Table 6, McDonald 1969). The estimated proportions are shown in Fig. 2, along with those for the underlying population as a whole. These latter values are simply area indices of abundance expressed as percentages of the sum of the indices for Main Lake areas.

The marking program of 1965–67 was designed specifically to compare wild and channel-produced fry. In Fig. 2, their distributions can be seen to be similar to each other and to the distribution of the total underyearling population. Some of the observed differences between wild and channel fish may be more apparent than real. For example, the proportions in session III, for 1966 and 1967, were calculated from a small number of mark recoveries (see Table 3), and considerable error is likely. On the other hand, differences seen in session I, 1965, were attributed to differences in times of lake entry between the two marked groups (McDonald 1969). The similarities, however, far outweight the differences and strongly support the conclusion that the origin of the fry, whether wild or channel, did not have any substantial effect on their distribution in the lake.

The programs of 1970 and 1971 in which fry from the Fulton and Pinkut systems were marked served two purposes. First, the

1970 and 1971 distributions of Fulton fish can be compared with that described above for prechannel years 1965–67. Second, the distribution and extent of mixing of juveniles from Fulton and Pinkut can be examined.

Fulton fry were distributed in much the same way in pre- and post-channel years (Fig. 2). The dispersal of most fry into southern lake areas continued in 1970 and 1971, confirming that this movement is a consistent feature of the Fulton stock. Distributions in session II were comparable as well, while those in session III remained variable.

Mixing of Fulton and Pinkut juveniles occurred in all three fishing periods. In session I, mixing was confined mostly to area 5, which is adjacent to Pinkut Creek. The limited dispersal of Pinkut fish compared with that of Fulton fish probably results from the relatively late time of lake entry by Pinkut fry (West 1968) and thus less time to disperse. The similarity in distribution of the two stocks during session II and to a lesser extent in session III is striking. The two stocks were found in almost equal proportion in all lake areas, indicating that they were distributed as a single population.

Comparisons of Size and Growth

Marked wild and channel juveniles

Data are available to compare the sizes of the two groups from fry migrant to smolt migrant stages (Table 5). Values for fry migrants were weighted to daily abundance and cannot be tested statistically but the means indicate little difference in length or weight. Mean lengths of wild fry were between 27.80 and 28.21 mm, while those for channel fry were between 27.21 and 28.31 mm. In 1966, wild fry were slightly longer and heavier. In 1967, channel fry were slightly longer but only equalled wild fry in weight. West (1978) reported the mean lengths of fry from the same two sources for the brood years 1965 and 1966. His data arose from samples of fry migrants drawn completely independently of this study. Differences in mean length were consistent with those observed for marked fry. West found that the mean lengths of wild and channel fry from the 1965 brood year were not significantly different ($P > 0.05$). However, in 1966, wild fry were found to be longer than their channel counterparts ($P = 0.002$).

Comparisons at subsequent stages reveal that channel fry were consistently smaller throughout the period of lake residence and again at time of seaward migration (Table 5; Fig. 3). While the differences were not very large (channel fish were 88–99 and 80–98% of wild fish in length and weight, respectively), in most cases the means were significantly different ($P < 0.05$).

On the other hand, growth rates of wild and channel fry were similar (Table 6). Fastest growth in length was reached between sessions I and II (July–August) when rates approached 1%/d. Growth in weight was greatest from time of lake entry to session II and varied from 2.7 to 3.4%/d. As would be expected, growth rates slowed in the fall and fell sharply over winter when growth in length was less than 0.1%/d and growth in weight did not exceed 0.21%/d. The overwinter rates may be a poor description of growth in that period. Probably, most growth would have occurred in late fall and/or early spring just before seaward migration.

Direct comparisons of the growth of wild and channel-produced juveniles were made by covariance analysis using sizes of marked fish recovered from sessions I, II, and III. This period, from late June or early July to October, spans most of the first growing season. The length and weight of individual mark recoveries were converted to natural logarithms. Recovery dates were assigned time values (days) based on May 1 equal to day 1. Results are summarized below (a = computed sizes of the fry (logarithms) on day 0 (April 30); b = instantaneous rates of increase in length and weight with 1 d as the unit of time; $^{**}P = 0.01$):

		Length				Weight				
				F value				*F* value		
Brood year	Source	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	df
1965	Wild	3.121	0.0069	58.26**	1.73					1 305
	Channel	2.962	0.0074							
1966	Wild	3.041	0.0083	33.54**	1.84	−2.49	0.0262	34.28**	2.01	1 399
	Channel	3.032	0.0076			−2.51	0.0239			
1967	Wild	3.056	0.0084	27.79**	0.01	−2.49	0.0269	25.29**	0.00	1 361
	Channel	2.992	0.0084			−2.71	0.0268			

Over the 3 yr there were no significant differences in the slopes (growth rates) of the regressions for wild and channel fish. Each year, however, the intercepts were significantly different, confirming that channel-produced underyearlings were consistently smaller than their wild counterparts.

This difference did not appear to have resulted from differences in initial size (of fry) or different growth rates but rather from different times of lake entry. The migrations of channel fry were consistently later than those of wild fry (by 9–14 d), and periods of growth in the lake prior to sampling in session I differed accordingly. Mean growing periods to session I were 44 and 32 d for wild and channel fry, respectively (from Table 6), giving wild fry a distinct advantage. For example, assuming an initial length of 28 mm and a growth rate of 0.008 mm/d (the approximate mean of observed values), the size a wild fry would attain by session I would be 39.80 mm, while that for channel fry would be 36.16 mm. The difference of 3.64 mm is close to the actual differences observed in the three brood-years used for the comparisons (Table 5). Since growth rates remained comparable at subsequent life history stages, the size advantage gained initially by wild fry was maintained through to seaward migration.

TABLE 5. Mean size of marked wild and channel juveniles from fry to smolt stages.

Brood year	Stage	No. in sample		Mean fork length (mm)			Mean weight (g)		
		Wild	Channel	Wild	Channel	t	Wild	Channel	t
1965	Fry	450	450	28.21	28.19				
	Session I	55	75	35.96	31.69	5.663***			
	Session II	51	75	52.88	47.12	2.077*			
	Session III	27	27	69.85	65.89	6.833***			
	Smolt	487	790	78.90	76.94	6.853***			
1966	Fry	1000	950	27.80	27.21		0.172	0.155	
	Session I	30	39	38.57	36.11	2.247*	0.645	0.517	2.280*
	Session II	79	134	63.37	58.57	4.256***	2.888	2.325	3.979***
	Session III	11	26	69.68	66.75	1.275	3.914	3.230	1.421
	Smolt	754	1222	80.42	78.22	8.450***	5.543	5.128	7.870***
1967	Fry	700	699	27.84	28.31		0.156	0.156	
	Session I	57	72	37.49	35.33	2.901**	0.550	0.441	2.810**
	Session II	45	38	60.91	56.97	2.630**	2.490	2.050	2.740**
	Session III	5	8	72.40	71.25	0.300	4.229	3.831	0.700
	Smolt	1228	1551	81.14	80.36	3.880***	5.158	5.038	2.910**

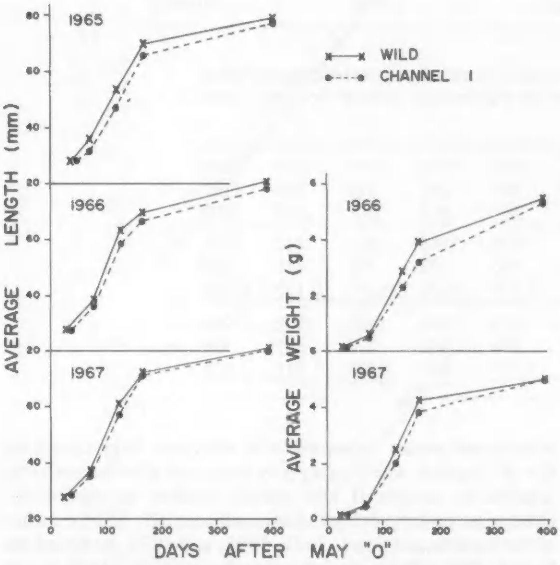

FIG. 3. Size comparisons of marked wild and channel juvenile sockeye, fry to smolt stage, 1965–67.

Juveniles in pre- and post-channel years

Size of fry migrants — Fry from Pinkut Creek and Fulton River and their associated spawning channels were sampled at frequent intervals during their downstream migration (Ginetz 1977). The samples of usually 50 fish were randomly subsampled in proportion to the abundance of fry migrants, and weighted mean lengths and weights of fry entering the main lake each year from these sources were calculated. Available data allow comparisons of two prechannel years (1965 and 1967) and seven postchannel years (1970–76). Annual mean lengths and weights ranged from 29.3 to 30.2 mm and from 0.135 to 0.154 g, respectively (Table 7). Although some significant differences between means occurred, there was no pattern over the years that would suggest differences between pre- and post-channel periods. In terms of length, fry from the two prechannel years were not significantly different from those in three of seven postchannel years. In terms of weight, fry from the 1966 brood were not significantly different from those of the postchannel years 1972 and 1974, and the 1965 mean did not differ significantly from those of six of the seven postchannel years.

There is evidence however, that fry in prechannel years tended to be heavier per unit length. It can be noted from the table that while their mean lengths were among the least, their mean weights were among the greatest. Stage of development of wild and channel migrants was compared (Table 7) using the index of Bams (1967) where

$$K_d = \frac{10\sqrt[3]{\text{weight in mg}}}{\text{length in mm}}.$$

Indices for 1965 and 1966 were greater than those for most other years, revealing that prechannel fry were less advanced and contained relatively large amounts of heavy (as compared with body tissue) yolk sac material.

Size of underyearlings — Mean sizes of underyearling in Main Lake areas 1–5 were compared. Two-way analysis of variance was applied to length data for each fishing session using years and areas as the two factors (Table A4). Significant differences among years and areas occurred in all three fishing periods. Interactions between areas and years were significant ($P < 0.001$), showing that differences among areas changed from year to year.

A more detailed analysis of each year's data and each session was undertaken using Duncan's multiple range test (Tables A5). During session I, underyearlings in area 1 were always larger than those in any other area. In the prechannel years (1965–67), underyearlings in area 2 or 5 were smallest and those in areas 3 and 4 were intermediate in size. In postchannel years, a distinct north–south gradient can be seen with mean lengths and weights decreasing progressively from area 1 to area 5. In session II, underyearlings in area 1 remained relatively large (6 of 7 yr). A north–south trend in size occurred in prechannel years 1966 and 1967 (whereas it was absent in session I) and in postchannel

TABLE 6. Instantaneous growth rates of marked wild and channel juveniles (SI, SII, SII = sessions I, II, and III).

Brood year	Stage	Central dates	t (d)	Growth in length		Growth in weight	
				Wild	Channel	Wild	Channel
1965	Fry–SI	June 6–July 11	35	0.0069			
		June 17–July 11	24		0.0034		
	SI–SII	July 11–Aug. 28	48	0.0080	0.0083		
	SI–SIII	Aug. 28–Oct. 16	49	0.0057	0.0068		
	SIII–smolt	Oct. 16–June 8	235	0.0005	0.0007		
1966	Fry–SI	May 29–July 17	49	0.0067		0.0270	
		June 6–July 17	35		0.0081		0.0344
	SI–SII	July 17–Sept. 6	51	0.0098	0.0095	0.0294	0.0295
	SI–SIII	Sept. 6–Oct. 14	38	0.0025	0.0035	0.0080	0.0086
	SIII–smolt	Oct. 14–May 27	225	0.0006		0.0016	
		Oct. 14–May 28	226		0.0007		0.0021
1967	Fry–SI	May 25–July 11	47	0.0063		0.0268	
		June 6–July 11	38		0.0058		0.0273
	SI–SII	July 11–Sept. 1	52	0.0093	0.0092	0.0291	0.0296
	SII–SIII	Sept. 1–Oct. 14	43	0.0041	0.0052	0.0123	0.0145
	SIII–smolt	Oct. 14–May 30	228	0.0005		0.0009	
		Oct. 14–May 29	227		0.0005		0.0012

TABLE 7. Mean length, weight, and K_d of newly emerged downstream migrant fry from the Pinkut and Fulton systems. Means that are underlined are not significantly different from each other ($P > 0.05$).

Brood year	1975	1965	1976	1966	1972	1971	1974	1973	1970
N	365	273	337	509	681	202	319	380	1135
Length (mm)	29.3	29.3	29.4	29.5	29.5	29.8	29.8	29.9	30.0
Brood year	1976	1970	1971	1974	1975	1965	1973	1972	1966
N	337	1135	202	265	365	272	380	681	509
Weight (g)	0.142	0.147	0.147	0.148	0.148	0.150	0.152	0.153	0.154
Brood year	1970	1974	1971	1976	1973	1975	1965	1972	1966
N	1135	265	202	337	380	365	272	681	509
K_d	1.756	1.766	1.770	1.775	1.783	1.803	1.808	1.811	1.815

years 1970 and 1972. The distribution of means in 1971 and 1976 differed from those in other years in that underyearlings in area 5 rather than being the smallest were either the largest or second largest. In session III, the distribution of means was similar in prechannel years and also in 1970 and 1972. In each of these years there was generally a progressive decrease in size from north to south. In 1971 and 1976, however, the reverse was true, with the largest underyearlings occurring in area 5 and the smallest in area 1.

The analysis clearly shows that the mean size of underyearlings in the Main Lake differed considerably from area to area in all fishing periods and in all years. Usually, the largest underyearlings were found in area 1 and the smallest in area 5, often with a progressive decrease in size from north to south. Exceptions to this pattern were seen in 1971 and 1976 when by fall (session III) a strong south–north gradient was established, exactly the reverse of other years.

Further examination of underyearling size in pre- and post-channel periods was carried out by comparing annual means for the Main Lake as a whole (areas 1–5 combined). Differences in mean length were tested (Table A6). In session I, underyearlings in postchannel years were significantly larger than those in prechannel years. As the season progressed, postchannel means continued to be relatively large except for the 1970 means, which changed in rank from third largest to the smallest in session II and second smallest in session III. Otherwise, ranking did not change substantially and the means of the postchannel years, 1971, 1972, and 1976, remained the largest. The differences were significant in session II but in session III, 1972 and 1976 means were not significantly different from that of 1965, the highest ranking prechannel mean.

Differences in mean weight could not be statistically tested, but the means were distributed over the years in much the same way as mean lengths, suggesting that in three of the four postchannel years, underyearlings were not only longer but also heavier. To examine this contention, length–weight relationships were compared (Table A7). Significant differences in length–weight relationships occurred among years. However, differences occurred at least as frequently within pre- and post-channel periods as they did between the two periods. In session I, only one of four coefficients for postchannel years was significantly different from those of prechannel years. In session II, no significant differences between the two periods were found, while in session III, differences occurred between combinations of pre- and post-channel years.

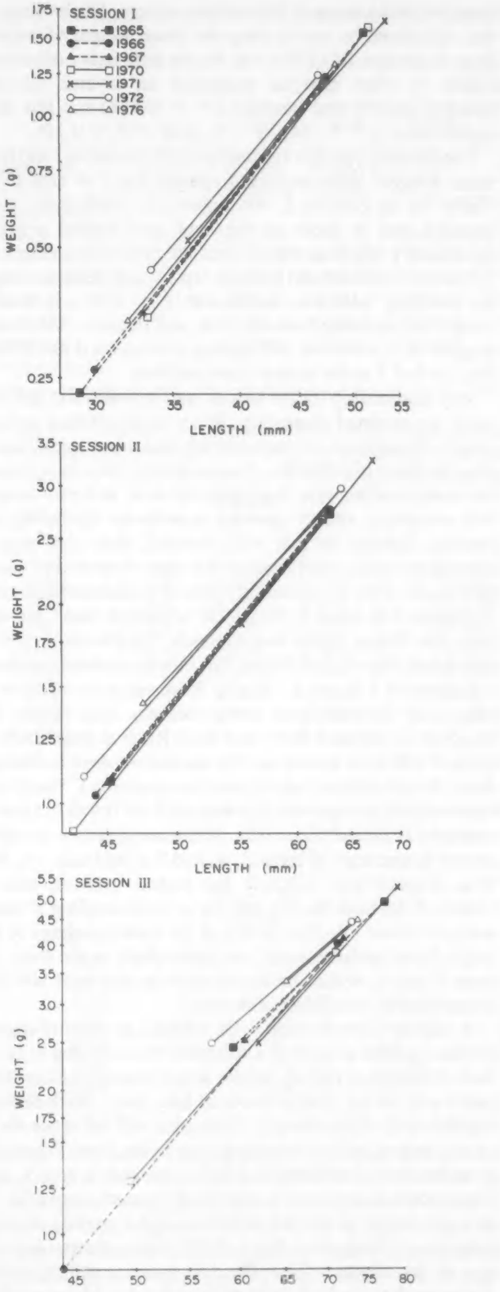

FIG. 4. Relation between length and weight of Main Lake underyearlings by brood years and fishing periods.

Differences and similarities in weight per unit length can be seen by inspection of the regression lines shown in Fig. 4. Most striking are the greater elevations of the lines for 1972 (session I) and 1972 and 1976 (sessions II and III). Postchannel underyearlings were not only longer in 3 out of 4 yr than prechannel underyearlings but in 2 yr (1972 and 1976), they were heavier per unit length.

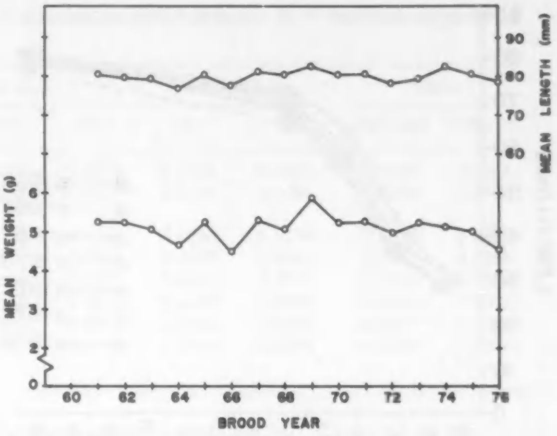

FIG. 5. Mean length and weight of Main Lake smolts, 1961–76 brood years.

Size of seaward migrants — Main Lake smolts were sampled daily during their annual migrations from Babine Lake. Mean lengths and weights were weighted to abundance (daily abundance estimates from tag and recovery procedures) to provide estimates of annual means for the brood years 1961–76. Mean length ranged from 76.72 to 82.57 mm and mean weight from 4.57 to 5.84 g (Fig. 5). During the 16-yr period no trend in size was apparent. Linear regressions of length and weight on brood years and smolt abundance were calculated with the following results:

	b	*F*
Years with weight	−0.0109	0.3399
Years with length	0.0537	0.3717
Abundance with weight	−0.0015	0.1330
Abundance with length	0.0050	0.0624

In all cases, slopes did not differ from zero ($P < 0.01$), demonstrating no significant change in size between pre- and post-channel periods.

Comparisons of annual growth rates — Mean weight and length at the various life history stages were plotted to illustrate annual growth patterns (Fig. 6). Dates shown are the midpoints of annual fry and smolt migrations and of sampling periods for underyearlings. Instantaneous growth rates were calculated to permit more precise comparison of growth among years (Table 8). Annual growth patterns were similar to these already described for marked fish with rapid growth in spring and summer slowing in fall and slowing still further over winter. In all but 1 yr (1972), relative increases in weight were greatest from May to July, and in all years relative increases in length were greatest from July through August. Growth rates in the periods between fry migration and session III, while variable, do not suggest any change from pre- to post-channel years. Rates for 1965–67 were all within the range of those observed in later years. However, overwinter growth rates in three of four postchannel years were relatively low, about one-half the rates in prechannel years. As a result of this slow overwinter growth, the

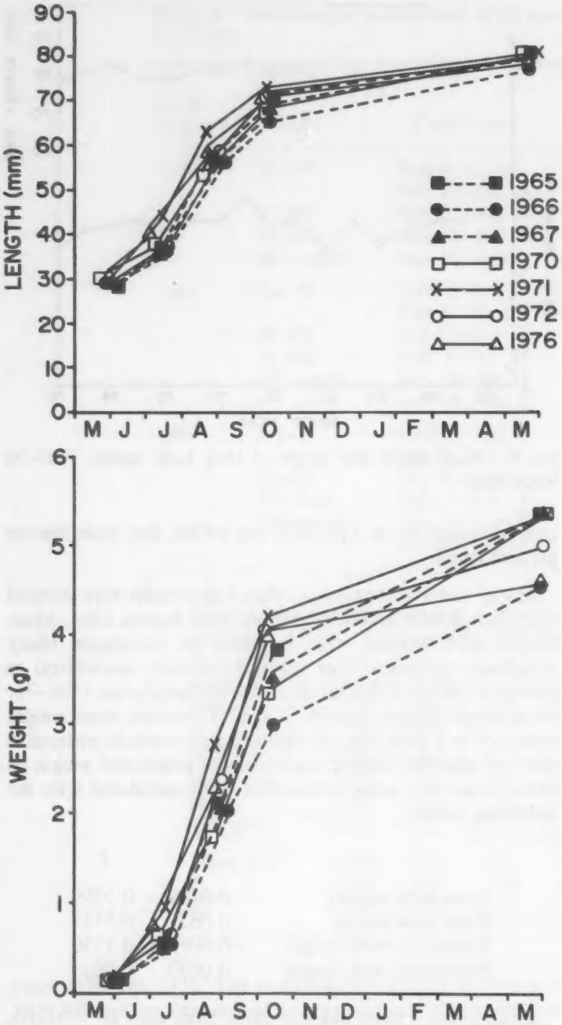

FIG. 6. Increase in mean length and weight from fry to smolt stage in Babine's Main Lake.

progeny of the 1971, 1972, and 1976 brood years that were large as underyearlings were comparable in size with those in other years by the time of seaward migration. In contrast, the progeny of the 1970 brood that were small as underyearlings, experienced fast growth over winter, and by the time of seaward migration they were amongst the largest.

Size and Density Relationships

The differences in overwinter growth rates noted above and some consistent trends in the distribution of underyearling size and density that were evident during the summer months suggest that density-dependent mechanisms may have been operative in the Main Lake. Overwinter growth rates were low in three postchannel years when, by fall, underyearlings were both relatively abundant and large in size. To test for compensatory growth, we regressed overwinter growth rates against an index of the biomass of fall underyearlings. The biomass index was calculated by multiplying the mean weight of underyearlings in session III (Table A6) by the lake index of abundance (Table 1). This analysis suggested an inverse relationship between growth and biomass ($r^2 = 0.528$) but fell short of significance ($t = 2.324$, $df = 5$, $0.05 < P < 0.10$).

For the early and late summer periods (sessions I and II), area mean weights were regressed against $\log_{10}$ of area densities (Table 9). In Session I, the regression coefficients were all negative and in three of the four postchannel years were significantly less than zero. When the probability values for all 7 yr were combined and a single test of significance computed, the resulting value was significant ($P < 0.01$), indicating an inverse relationship between size and density. There was no suggestion of a similar relationship in sessions II and III and, in fact, in 4 of 7 yr the slopes were positive.

Any relationship (or the lack of one) between size and density must be examined cautiously. It was demonstrated earlier that change throughout summer and fall was a consistent feature of underyearling distribution. Consequently, there is no assurance that underyearling size in a particular area, at a particular time, will accurately reflect growing conditions (including underyearling density) in that area. Instead, their size may more accurately reflect conditions in the area or areas they occupied previously. This is particularly true of underyearlings sampled in session I in areas 3–5, which contained many immigrants from the Fulton River and channels. McDonald (1969) estimated that dispersal of Fulton fish into these areas occurred at a rate between 1.0 and 1.3 km/d. New estimates of their travel rates were derived from mark–recovery data (Table 4) and based on the distance from the Fulton River at which 50% of the marked fish were found and the number of days between mid-dates of mark releases and recoveries in session I. Travel rates of eight marked groups over 5 yr ranged from 0.7 to 1.3 km/d and averaged 1.0 km/d (Table 10). At this average rate, travel to the nearest boundaries of areas 3, 4, and 5 would take 16, 36, and 59 d, respectively. Because the period between lake entry (mainly from mid-May to mid-June) and sampling in session I was only about 40–70 d, many of the underyearlings of Fulton origin found in these areas, and particularly in the more distant areas 4 and 5, would be recent arrivals and their size largely determined by conditions enroute.

A further complication with respect to density-dependent effects apparent in session I can result from mixing of juveniles from different spawning stocks when these juveniles differ in initial size (as fry) and in times of lake entry. Such differences together with differences in abundance will influence the mean size of underyearlings observed later in the lake. The mixing of juveniles from the Fulton and Pinkut systems in area 5, and to a lesser extent in area 4, was confirmed by mark recoveries (Table 4) and is surely an annual feature of underyearling distribution in session I. Data from West (1978) allow comparisons of the size of fry migrants from the two systems and of their peak migration dates in the four postchannel years. Mean weights and peak migration dates of fry produced from the natural spawning grounds and spawning channels were weighted according to the number of fry produced from each to arrive at an overall mean value for each system (Table 11). Fry from the Pinkut system were consistently smaller than those from Fulton and migration was later except in 1976 when, according to West, rising water temperatures and discharge resulted in an unprecedented early migration. While the differences in mean size were not large, in combination with their later time of lake entry (except for 1976),

TABLE 8. Instantaneous growth rates for Main Lake juveniles (G_W = instantaneous growth in ln g/d; G_L = instantaneous growth in ln mm/d).

		Brood year							Mean	
		1965	1966	1967	1970	1971	1972	1976	1965–67	1970–76
Emerging fry–session I (May–July)	G_W	0.0365	0.0291–	—	0.0270	0.0368	0.0266	0.0433	0.0328	0.0334
	G_L	0.0064	0.0048	—	0.0046	0.0077	0.0046	0.0080	0.0056	0.0062
Session I–II (July–Aug)	G_W	0.0284	0.0272	0.0284	0.0256	0.0256	0.0290	0.0256	0.0280	0.0265
	G_L	0.0092	0.0082	0.0089	0.0079	0.0086	0.0099	0.0082	0.0089	0.0086
Session II–III (Aug.–Oct.)	G_W	0.0122	0.0099	0.0123	0.0134	0.0085	0.0149	0.0121	0.0115	0.0122
	G_L	0.0042	0.0040	0.0043	0.0048	0.0030	0.0049	0.0041	0.0041	0.0042
Session III–smolt run (Oct.–June)	G_W	0.0014	0.0018	0.0019	0.0020	0.0010	0.0009	0.0005	0.0017	0.0011
	G_L	0.0006	0.0007	0.0008	0.0007	0.0004	0.0004	0.0004	0.0007	0.0005

TABLE 9. Regression coefficients (b) of mean weight and density of underyearlings in Main Lake areas. Also shown are the coefficients of determination (r^2) and the probability of the regression coefficients being equal to zero (P).

Brood year	Session I			Session II			Session III		
	b	r^2	P	b	r^2	P	b	r^2	P
1965	−0.307	0.192	9,468	+0.082	0.009	>0.750	−0.388	0.035	>0.750
1966	−0.205	0.552	0.146	+0.309	0.082	0.663	+1.132	0.105	0.612
1967	−0.137	0.502	0.183	+0.344	0.074	0.678	−0.155	0.049	0.728
1970	−0.410	0.988	<0.0001***	−0.000	0.000	>0.750	+0.130	0.042	0.742
1971	−0.223	0.651	0.083	−0.178	0.026	>0.750	−0.465	0.014	>0.750
1972	−0.249	0.954	0.002**	+0.662	0.198	0.462	+0.825	0.253	0.407
1976	−0.361	0.905	0.006**	−0.083	0.058	0.505	+0.108	0.012	>0.75
$-2\Sigma \ln P$			50.217***			1.202 (NS)			2.166 (NS)

TABLE 10. Estimated travel rates of marked Fulton River and channel fry into southern lake basins.

Brood year	Middates			Time out (d)		Distance traveled (km)		Travel time (km/d)	
	Marked fry release								
	River	Channel	Recoveries	River	Channel	River	Channel	River	Channel
1965	June 6	June 17	July 11	35	24	35.6	16.1	1.0	0.7
1966	May 29	June 12	July 17	49	35	46.9	46.9	1.0	1.3
1967	May 25	June 5	July 11	47	36	46.9	35.6	1.0	1.0
1970		May 24	July 8		45		46.9		1.0
1971		May 25	July 13		49		58.7		1.2

the size that Pinkut fry would attain by session I would be considerably less than that of Fulton fry, with the result that the mean size of underyearlings in areas of mixing (mostly in area 5) would be less than that observed in areas occupied only by Fulton fish. The extent of this reduction cannot be quantified with available data. It will certainly vary from year to year depending on size and time differences at lake entry and the relative abundance of the two stocks.

The influence of progeny from other spawning stocks on mean size is even less certain. Fry from numerous small streams tributary to the Main Lake contribute to the underyearling population. However, their spawning stocks and resulting fry outputs are small relative to those of Fulton and Pinkut and any effect on underyearling size would be small as well.

There is a possibility, however, that progeny from the large spawning stock of the Babine River and that of the Morrison River may emigrate to the Main Lake and influence mean size, particularly in area 1, which lies immediately uplake of North and Morrison arms. Both mark–recovery data and abundance indices have demonstrated that this area is sparsely populated in

TABLE 11. Comparisons of size and migration times of sockeye fry from the Fulton and Pinkut systems.

Brood year	Average weight (g)		Peak migration date	
	Fulton	Pinkut	Fulton	Pinkut
1970	0.149	0.141	May 18	May 28
1971	0.148	0.138	May 27	May 31
1972	0.154	0.152	May 27	May 29
1976	0.143	0.136	May 25	May 5

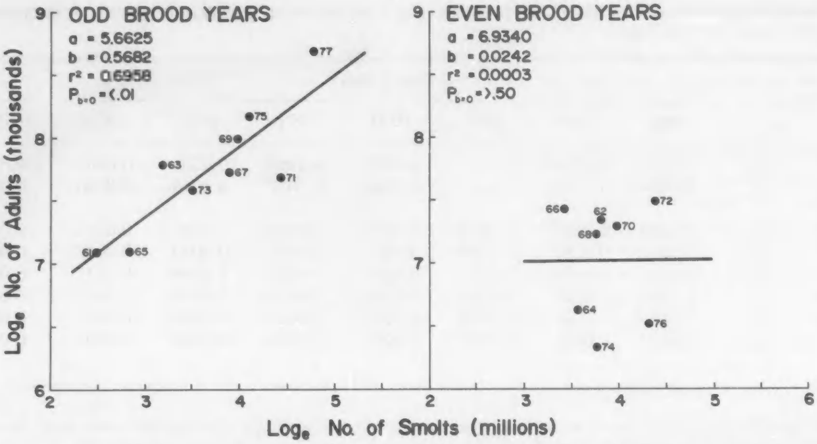

FIG. 7. Relation between smolt outputs and adult returns of Babine Lake sockeye for even- and odd-numbered brood years.

TABLE 12. Mean lengths (mm) and weights (g) of underyearlings in each lake basin. Mean lengths underlined are not significantly different from each other ($P > 0.05$).

Brood year	Basin	Session I Main Lake	 North Arm	 Morrison Arm
1966	Mean weight	0.50	—	1.52
	Mean length	36.0	48.6	50.7
1967	Mean weight	0.47	1.18	1.19
	Mean length	35.6	46.6	47.4
1970	Mean weight	0.54	0.89	—
	Mean length	37.5	43.6	—
1971	Mean weight	0.96	1.26	1.52
	Mean length	44.1	48.0	51.7
1972	Mean weight	0.63	1.14	1.59
	Mean length	37.3	44.6	49.9
1976	Mean weight	0.65	0.81	0.88
	Mean length	38.9	41.6	42.0

session I by juveniles from the Fulton system. The movement of only small numbers of fish from the two arms into area 1 could have a strong influence on the mean body size of the composite population.

As noted earlier, McCart (1967) observed during May and June schools of fry migrating from the Babine River as far as 32 km uplake and only 11 km from the Main Lake. If the dispersal of these fry is as far ranging and as rapid as that observed for Fulton fry, the presence of some Babine River fry in area 1 by early June could be expected. The presence of fry from the Morrison River only 10 km away is even more likely.

Data are available from six brood years to provide comparisons of underyearling size in the two lake arms and Main Lake during session I (Table 12). North Arm and Morrison Arm fish were substantially and significantly larger with mean lengths between 107 and 141% those of Main Lake fish. The presence in area 1 of relatively larger underyearlings from one or both of the lake arms could account either completely or at least in part for the large mean size observed in this area relative to other Main Lake areas.

The evidence for stock mixing in area 1 is far from conclusive but is sufficient to suggest that the relatively large size of underyearlings in this area may be the result of stock mixing rather than the effect of low population density. While the situation in area 1 remains unclear, there is more convincing evidence that the small size of underyearlings in densely populated area 5 is due at least in part to the mixture of Fulton and Pinkut stocks.

Adult Returns

Smolts outputs and adult returns by age group and in total from prechannel brood years (1961–67) and postchannel brood years (1970–71) were compared (Table 13). Preliminary estimates for 1977 are courtesy of R. Kadowaki (Fisheries and Oceans, Prince Rupert, B.C., personal communication). Remaining estimates are from various Department of Fisheries and Oceans sources.

The mean total return of 2 249 700 adults in the postchannel period exceeded the prechannel mean by 667 000. The means, however, were not significantly different ($P > 0.20$). Also, no significant difference was seen in mean numbers of 4-yr-olds (1.2) and 5-yr-olds (1.3). However, 3-yr-old jack sockeye (1.1) were more abundant in the postchannel period ($P < 0.05$). When expressed as a percentage of the total return, the mean proportion of jacks produced in the postchannel period was 10.5% as compared with 5.9% in the earlier period, a significant difference ($t = 2.627$, $P < 0.055$).

Peterman (1978, 1982) concluded that the relationship between smolt outputs and adult returns was density dependent with no significant increase in returns when smolt outputs increased. Peterman also pointed out that the survival rates of smolts produced from odd-numbered brood years were usually greater than those for smolts from even-numbered brood years. This difference is readily apparent by inspection of rates given in Table 13. The average survival rate of 6.4% in odd-numbered brood years was more than double the average rate of 2.6% in even-numbered brood years ($t = 3.663$, $P < 0.005$).

In view of the apparently different smolt to adult relationship between even- and odd-year broods, we have examined each separately. A strong positive relationship was found between smolt abundance and adult returns from the odd-numbered

TABLE 13. Babine sockeye smolt and adult production, 1961–77 brood years.

Brood year	Smolts (millions)			Adult returns (thousands)				Smolt-to-adult survival (%)
	Main Lake	North Arm	Total	1.1	1.2	1.3	Total	
1961	5.78	6.75	12.53	60.0	649.3	488.8	1198.1	9.6
1962	29.38	16.54	45.89	64.0	548.2	940.9	1553.1	3.4
1963	19.16	4.51	23.67	182.0	975.2	1275.9	2433.2	10.3
1964	13.78	21.53	35.31	29.3	199.6	510.7	739.7	2.1
1965	6.84	9.73	16.57	53.4	746.0	402.4	1201.8	7.3
1966	18.10	12.79	30.89	154.0	822.8	704.1	1680.9	5.4
1967	24.18	22.01	46.19	166.0	1040.7	1067.0	2273.6	4.9
1968	34.63	8.38	43.01	54.6	369.5	963.5	1387.6	3.2
1969	39.20	13.31	52.51	258.7	1131.8	1505.2	2895.7	5.5
1970	45.56	8.78	54.34	233.4	849.2	370.5	1453.1	2.7
1971	73.98	14.77	88.75	254.3	1104.0	798.6	2157.0	2.4
1972	61.13	19.00	80.13	137.0	548.2	1092.9	1778.1	2.2
1973	27.43	6.62	34.05	255.5	958.4	739.3	1953.1	5.7
1974	36.12	6.86	42.98	45.4	223.1	294.3	562.8	1.3
1975	51.01	10.03	61.04	296.3	2332.5	838.7	3467.5	5.7
1976	70.92	5.04	75.96	93.4	223.2	354.4	671.0	0.9
1977	99.19	9.03	108.22	233.9	2714.7	2240.0	5955	5.5
1961–67 mean			30.13	101.2	711.7	770.0	1582.9	6.1
1970–77 mean			68.18	193.7	1119.2	841.1	2249.7	3.3
t			3.628	2.269	1.111	0.267	0.954	2.764
P			<0.05	<0.05	>0.20	>0.50	>0.20	<0.025

brood years (Fig. 7). The relationship, when tested by the conservative Varley and Gradwell (1963, 1968) method, as used by Peterman (1978), is curvilinear, indicating density dependence with the rate of adult returns decreasing as smolt abundance increases. However, the degree of density dependence is small enough to permit an increasing surplus of returning adults from smolt outputs several times the preenhancement level. For example, the predicted return from the postchannel average smolt output of about 70 million is 3 million adults. Allowing for brood stock requirements (no more than 1 million spawners), the surplus (available catch) of 2 million more than exceeds the initial target of the enhancement program.

While the productivity of the odd-numbered brood years has met expectations, even-numbered brood years have performed poorly. Adult returns varied widely but did not indicate any response (positive or negative) to smolt abundance within the range observed.

Discussion

There is considerable evidence to show that the basic assumptions regarding juvenile production were valid or nearly so. The artificial spawning channels proved to be effective producers of sockeye fry with egg-to-fry survival rates close to the 40% anticipated. One shortcoming was the lack of response in production to flow control over the formerly natural spawning beds of Fulton River and Pinkut Creek. Some increase in egg-to-fry survival was expected (the amount was never specified) but survival rates did not increase. The end result was an average increase in fry output into the Main Lake of 106 million, less than the 125 million projected, but still sufficient to increase the juvenile population nearly threefold.

Two lines of evidence are available to examine the hypothesis that channel-produced fry were as viable as wild fry. Comparison of marked fry revealed little difference in the survival rates of the two types through to the smolt stage. The small differences observed were probably more apparent than real, reflecting sources of error inherent in marking and recovery methods. Results from marking and recovery were confirmed by observed changes in the total abundance of Main Lake juvenile populations from prechannel to postchannel years. The nearly threefold increase in mean fry output was followed by roughly equivalent increases in the abundance of underyearlings and seaward migrating smolts.

Comparison of the size and growth rates of 1965–67 brood year juveniles produced from the Fulton River (wild fry) and the first Fulton River spawning channel revealed that growth rates were similar, but channel-produced fish were smaller on the average as underyearlings and again as smolts. The difference was attributed to later fry migrations from the channel and consequently a reduced growing period in the lake.

The 1965–67 comparison, however, cannot be considered representative of later years. With flow control in 1968, and with the large second Fulton River channel and the Pinkut Creek channel in operation, all sockeye production in the two systems was subject to some form of manipulation influencing fry migration time. West (1978) noted flow control, increased water temperatures, and adult "loading" (i.e. manipulation of times of entry of parent spawners into the facilities) as factors influencing fry migration time. Data from West (1978, Table 8) show that since 1970, migrations of channel fry have generally peaked during the 3rd or 4th wk of May or about 2–4 wk earlier than in the 1965–67 period. The increased growing period in the lake provided by earlier migrations served to eliminate any disadvantage in size of channel-produced fish. As a result, underyearlings in postchannel years were equal to or exceeded the size of prechannel underyearlings and their mean size as smolts was not significantly different.

Lake Capacity

Johnson (1958, 1961, 1965b), after comparing the size and density of underyearlings in various parts of the Babine Lake system, found an inverse relationship between size and density. He concluded that growth was density dependent, with food supply and also possibly space the limiting factors. The relatively low density and large size of underyearlings he observed in the Main Lake basin led to the hypothesis that the Main Lake nursery area was underutilized and could support a much larger juvenile population.

Johnson's interpretation of compensatory growth depended on his assumption that dispersal of young from their natal streams was limited and that once pelagic, they remained as discrete populations in discrete lake basins. While this may be the case in a very general sense in that the interchange of Main Lake and North Arm population does not appear to be very great (McDonald 1969 and unpublished data), fry in the Main Lake dispersed widely from their natal streams, and McCart (1967) observed that fry from the Babine River dispersed throughout much of the North Arm. The situation with respect to Nilkitkwa Lake, which separates the upper and lower Babine River spawning grounds, is less clear but judging by McCart's observations of the size and movements of Babine River fry, the population in Nilkitkwa Lake is largely transitory and most fry eventually migrate upstream into the North Arm.

Movement patterns similar to those in the Babine system have been reported in other sockeye-producing lakes. Hartman and Burgner (1972), when reviewing sockeye production in Alaskan systems, noted widespread fry dispersal in each of the five Wood Rover lakes and also in very large Lake Iliamna. In the Naknek River system, which consists of a chain of four lakes, these authors reported that both interbasin (i.e. within lake) and interlake migrations occurred. Goodlad et al. (1974) reported fry dispersal followed by changes in underyearling distribution in Fraser, Chilko, and Shuswap lakes of the Fraser River drainage.

Two of the reports cited above included estimates of underyearling size observed at various locations in the nursery area. McCart (1967), after sampling in early July, found a direct relationship between the average length of underyearlings in Babine's North Arm and the distance from their point of origin (Babine River). This size trend then broke down, suggesting that considerable mixing was taking place. A similar trend in size with distance was reported by Hartman and Burgner (1972) in the Wood River lakes. Samples taken in late summer revealed that average length of sockeye juveniles increased from the west end (where most fry originated) to the east end of these lakes. They concluded that size differences within each lake were the result of more widespread dispersal of the older and larger fish, which were the first to emerge from the spawning beds. Growth rates calculated from these data would be apparent only and not representive of different rates for different lake areas.

Widespread dispersal of growing juveniles appears to be characteristic of moderate to large-sized lake basins. In the two documented cases where the fry originated from a single source (or at least a fairly localized one), there was a trend of increasing size with distance "uplake." The dispersal of fry from their point of lake entry where they would be most abundant (at least initially) into distant and less populated lake areas would result in a second trend; that of decreasing population density with distance from their source. A similar trend can be seen in Johnson's (1958, 1961, 1965b) North Arm data. The trends of increasing size and decreasing density with distance when combined would produce an inverse relationship between size and density, which could be construed wrongly as density effects on growth.

There are good grounds for caution when interpreting size and density relationships that may be seen when comparing data obtained from different areas within a nursery lake. In Babine's Main Lake and probably also in the North Arm and in Nilkitkwa Lake, density effects will be confused by fry dispersal followed by changes in distribution of the population during their growing period. At any one time and place of sampling, underyearling size will be the net result or balance of densities, food supply, and other factors influencing growth that were encountered previously. The situation in the Main Lake is even further confused by the mixing of juvenile stocks that differ in the size of fry and times of lake entry.

These complexities preclude the use of current information to arrive at a point estimate of the carrying capacity of the Main Lake. However, by using the criteria of juvenile size and survival rate, we can indicate whether this capacity has been exceeded by the larger postchannel population. After a nearly threefold increase in average abundance, underyearlings remained at least comparable in size and no significant change in the mean size of smolts was found to occur. Two independent lines of evidence were available to compare fry-to-smolt survival rates of pre- and post-channel populations. The mean rates based on total fry and smolt outputs of 26.5 and 30.7% were not significantly different. Comparison of the rates calculated for marked fry supported this conclusion. The absence of any reduction in size and survival rate supports the hypothesis that the Main Lake nursery area was capable of supporting the larger juvenile populations. However, it should be noted that in years when, by fall, juveniles were relatively large in size and number, overwinter growth tended to be slowed, suggesting that the overwinter carrying capacity of the lake may have been approached.

Adult Returns

The final assumption was that larger juvenile outputs would result in increased adult returns. The response from odd-numbered brood years has been about as expected. While the relationship between smolt output and adult return is curvilinear, it still allows a large surplus of adults from smolt outputs more than two or three times the preenhancement level. Gains from odd-numbered brood years, however, have been largely offset by the consistently low productivity of even-numbered brood years.

Available evidence does not suggest that the difference in even- and odd-year productivity originates in the lake. As noted by Peterman (1982) and Ricker (1982), there is no consistent difference in the mean size of smolts from even- and odd-year broods, which might explain different survival rates either en route to the sea or in it. The only other available measure of smolt quality that might bear on their survival is the degree of infestation by the internal parasite *Eubothrium salvelini*. This parasite is found every year in large numbers of Babine smolts. Its presence is associated with reduced size and vigor of the host (Smith 1973). Annual infection rates recorded by Smith and updated by N. Boyce (Fisheries and Oceans, Ottawa, Ont., personal communication) do not reveal any significant difference in mean rates of 33 and 29% ($P = 0.50$) for even- and odd-numbered brood years, respectively. While the incidence of *Eubothrium* may reduce the marine survival of Babine results, as Smith suggested, the presence of the parasite does not appear to account for the difference in odd- and even-year survival rates.

Peterman (1982) suggested that the marine survival of Babine smolts is density dependent and, further, that this dependence may be due to interaction with pink salmon (*Oncorhynchus gorbuscha*). Pink salmon have an invariable 2-yr life cycle, and along the north coast of British Columbia they are generally more abundant in even-numbered years. Peterman suggested two likely mechanisms. Large populations of juvenile pinks (from even-year parents) may serve as a buffer to predation on odd-year broods of sockeye smolts. These same pink salmon as incoming adults may actively prey on the outgoing even-year broods of sockeye smolts. Ricker (1982) also considered the possibility of predation of adult pink salmon but pointed out the difficulty of reconciling this hypothesis with past highly successful even-year broods of sockeye. There is of course no certainty that the even- and odd-year phenomenon observed in Babine sockeye during the past 20 yr or so existed during the earlier history of the run. Returns up to 1919 were characterized by a distinct 5-yr cycle of abundance and through the 1930's and 1940's by a 4-yr cycle (Larkin and McDonald 1968). It is difficult to relate either a 4- or 5-yr cycle with consistent superiority of even- or odd-numbered brood years.

Obviously, further information is required to clearly identify the mechanisms that are currently suppressing Babine sockeye production from even-numbered brood years. In the meantime, alternate management strategies should be considered. The current practice of attaining large brood stocks and smolt outputs from both even and odd years has not provided the expected increase in adult returns and shows little promise of doing so in the future. Returning to entirely natural production is one strategy that could be considered but one that would probably be politically unacceptable and possibly biologically unrealistic. Manipulation of brood stocks since the enhancement program began 17 yr ago has no doubt altered some of their biological characteristics that bear on reproduction. The difference in times of fry migration resulting from manipulating the "loading" of parent spawners was noted earlier. Such changes could result in decreased survival rates and even lower adult returns if enhancement facilities were abandoned.

A second strategy would be to make the best of the current even- and odd-year phenomenon until such time as the factors suppressing odd-year productivity are identified and corrective measures implemented. Under this strategy, odd-year brood stocks and smolt outputs would be maintained at current leves or even increased to take full advantage of their high productivity. In the relatively unproductive even years, brood stocks (and thus, resulting smolt outputs) would be reduced and then maintained at a moderate level by appropriate regulation of the fishery. In this way, more of the 5-yr-old adults from productive even-year broods but returning in even-numbered years could be added to the catch.

Whatever strategy may be adopted, it seems imperative that it proceed on an experimental basis and with close monitoring of the Babine stocks. Only in this way can adverse effects on the stocks be detected and ameliorated should the strategy be inappropriate. Close monitoring will also be required to identify future opportunities to increase production.

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Appendix

Tests for differences in density, abundance, and body size of underyearling sockeye among lake areas and among years are presented.

Density and Abundance

Estimates of the relative density and abundance of underyearlings in the five Main Lake areas were based on catch per unit effort by seine-net. If it is assumed that underyearling availability and gear efficiency remains constant, then catch per unit effort will be proportional to density. Each estimate of density was usually based on 10 sets. Catches were transformed to $\log_{10}$ to normalize their distribution.

Table A1. Two-way analysis of variance of estimated area density and abundance in the Main Lake using years and lake areas as the independent factors.

			F	
Source	df	Fishing period	Density	Abundance
Years	6	Session I	19.61***	19.65***
Areas	4		107.57***	12.08***
Interaction	24		1.52 (NS)	1.51 (NS)
Within	295			
Years	6	Session II	10.62***	10.47***
Areas	4		11.66***	28.66***
Interaction	24		2.80***	2.75***
Within	349			
Years	6	Session III	32.63***	31.49**
Areas	4		1.78 (NS)	22.12***
Interaction	24		2.10**	2.08**
Within	324			

Comparisons of density and abundance were made only within fishing sessions because seasonal changes in the availability of underyearlings to the gear could be expected to occur from one session to another due to increased fish size and possible changes in behavior.

Differences among lake area densities were tested by analysis of variance using years and areas as treatments (Table A1). This was followed by a multiple pairwise comparison of means (Table A2) using Duncan's multiple range test (Duncan 1955).

Because lake areas differed in size, area densities could not be used directly to estimate relative abundance. Instead, an area index was calculated by weighting catches by lake surface area and then finding the geometric mean. Differences among area indices were then tested by analysis of variance (Table A1) and Duncan's multiple range test (Table A3).

An index of abundance for the five main lake areas combined (as given in Table 1) was derived by summing areas indices and dividing by a constant to reduce the indices to a convenient number.

Size

The same statistical procedures were used to test for differences in underyearling length. Two-way analysis of variance showed that significant differences occurred among lake areas and years (Table A4). This was followed by tests for differences among lake areas during each fishing session each year (Table A5). Finally, mean underyearling lengths for the Main Lake as a whole (areas 1–5 combined) were tested for differences in pre- and post-enhancement years (Table A6). These means were calculated after subsampling lake area samples in proportion to abundance indices.

The relationship between length and weight was examined by regression analysis using logarithms of mean lengths and weights of underyearlings sampled from catches made in usually 50 sets each fishing session (Table A7). Differences in the relationship among years were tested by covariance analysis and the simultaneous test procedure (Sokal and Rohlf 1969).

TABLE A2. Geometric mean catch per set for Main Lake areas during three fishing periods. Means that are underlined are not significantly different from each other ($P = 0.05$).

Brood year		Lowest				Highest
				Session I		
1965	Area	1	2	3	4	5
	Mean	15.8	21.1	94.6	173.2	185.2
1966	Area	1	2	3	5	4
	Mean	12.5	45.9	103.5	161.8	249.2
1967	Area	1	2	3	5	4
	Mean	17.9	40.1	214.2	231.7	292.2
1970	Area	1	2	3	4	5
	Mean	19.5	100.1	192.9	237.6	381.9
1971	Area	1	2	3	4	5
	Mean	54.2	131.1	276.0	346.3	1576.8
1972	Area	1	2	3	4	5
	Mean	26.3	165.9	265.8	377.0	1067.6
1976	Area	1	2	3	4	5
	Mean	38.7	231.5	483.5	545.8	547.9
				Session II		
1965	Area	1	5	2	4	3
	Mean	31.9	49.4	57.6	110.5	153.7
1966	Area	1	5	3	2	4
	Mean	36.3	37.1	71.0	79.7	175.4
1967	Area	5	3	1	2	4
	Mean	64.9	74.9	120.4	130.6	311.3
1970	Area	5	1	3	2	4
	Mean	63.3	93.6	121.8	146.6	516.6
1971	Area	3	5	2	1	4
	Mean	125.9	183.6	261.3	419.6	506.2
1972	Area	5	1	3	4	2
	Mean	117.2	143.6	158.8	218.1	245.3
1976	Area	2	3	1	5	4
	Mean	36.7	71.0	224.4	357.8	531.7
				Session III		
1965	Area	1	4	3	5	2
	Mean	12.5	13.9	20.2	25.1	43.2
1966	Area	5	1	2	3	4
	Mean	20.2	25.0	26.7	33.2	43.8
1967	Area	1	2	5	4	3
	Mean	10.0	16.4	22.0	27.6	34.7
1970	Area	1	5	2	3	4
	Mean	54.7	67.2	62.9	216.5	244.5
1971	Area	3	2	5	1	4
	Mean	52.5	74.1	81.6	97.0	114.7
1972	Area	3	5	2	4	1
	Mean	63.4	68.2	100.4	143.3	162.5
1976	Area	3	1	2	4	5
	Mean	84.1	114.4	142.8	182.5	223.9

TABLE A3. Area index (of abundance) for Main Lake areas during fishing periods. Indices that are underlined are not significantly different from each other ($P = 0.05$).

Brood year		Lowest				Highest
				Session I		
1965	Area	1	2	3	5	4
	Mean	188	871	1115	2589	3115
1966	Area	1	3	2	5	4
	Mean	146	1242	1919	2262	4484
1967	Area	1	2	3	5	4
	Mean	210	1678	2569	3226	5253
1970	Area	1	3	2	4	5
	Mean	230	2314	4183	4275	5344
1971	Area	1	3	2	4	5
	Mean	645	3301	5495	6222	22065
1972	Area	1	3	4	2	5
	Mean	313	3187	6783	6956	14936
1976	Area	1	3	5	2	4
	Mean	463	5800	7619	9680	9817
				Session II		
1965	Area	1	5	3	4	2
	Mean	381	685	1840	1975	2342
1966	Area	1	5	3	4	2
	Mean	432	512	846	3152	3341
1970	Area	5	1	3	2	4
	Mean	881	1110	1449	6043	9282
1971	Area	3	5	1	4	2
	Mean	1509	2558	5028	9105	10958
1972	Area	5	1	3	4	2
	Mean	1627	1698	1859	3908	10261
1976	Area	3	2	1	5	4
	Mean	846	1521	2671	4986	9564
				Session III		
1965	Area	1	4	3	5	2
	Mean	148	233	238	347	1769
1966	Area	5	1	3	4	2
	Mean	253	284	383	786	1093
1967	Area	1	5	3	4	2
	Mean	91	303	413	481	685
1970	Area	1	5	3	2	4
	Mean	651	853	2592	1616	4399
1971	Area	3	5	1	4	2
	Mean	629	1131	1154	2059	3094
1972	Area	3	5	1	4	2
	Mean	759	942	1948	2575	4202
1976	Area	3	1	5	4	2
	Mean	1006	1370	3120	3282	5984

TABLE A4. Two-way analysis of variance of the lengths of underyearlings resident in the main lake areas using years and areas as the independent factors.

Source	df	SS	MS	*F*
Session I				
Years	6	65 097.64	10 849.61	395.284***
Areas	4	52 662.88	13 165.72	479.667***
Interaction	24	22 746.75	947.78	34.531***
Within	13 962	383 223.34	27.45	
Session II				
Years	6	55 687.78	9 281.30	164.574***
Areas	4	29 184.75	7 296.19	129.375***
Interaction	24	31 476.75	1 311.53	23.256***
Within	17 121	965 552.10	56.39	
Session III				
Years	6	56 587.31	9 431.22	157.333***
Areas	4	6 881.78	1 720.44	28.701***
Interaction	24	32 782.81	1 365.95	22.787***
Within	13 109	785 806.00	59.94	

TABLE A5. Mean lengths (mm) and weights (g) of underyearlings resident in each Main Lake area. Mean lengths that are underlined are not significantly different from each other ($P > 0.05$).

	Smallest					Largest
	Session I					
1965	Area	2	5	3	4	1
	Sample size	255	394	376	350	101
	Mean weight	0.32	0.50	0.52	0.60	1.25
	Mean length	32.0	35.6	37.5	38.1	48.9
1966	Area	5	2	3	4	1
	Sample size	500	260	490	500	154
	Mean weight	0.43	0.45	0.51	0.53	0.78
	Mean length	34.5	34.5	36.5	37.0	40.4
1967	Area	5	2	4	3	1
	Sample size	500	466	500	500	217
	Mean weight	0.46	0.45	0.46	0.49	0.70
	Mean length	34.9	35.2	35.7	36.1	40.5
1970	Area	5	4	3	2	1
	Sample size	201	200	200	200	157
	Mean weight	0.45	0.52	0.53	0.64	0.97
	Mean length	35.6	37.3	37.4	39.8	43.8
1971	Area	5	4	3	2	1
	Sample size	199	220	180	200	190
	Mean weight	0.89	0.91	1.03	1.24	1.14
	Mean length	43.1	43.1	45.6	45.9	46.7
1972	Area	5	3	4	2	1
	Sample size	498	500	499	500	267
	Mean weight	0.54	0.65	0.70	0.72	0.95
	Mean length	35.6	37.7	38.7	39.3	42.9
1976	Area	5	4	3	2	1
	Sample size	879	1002	1000	883	46.0
	Mean weight	0.50	0.64	0.67	0.73	1.01
	Mean length	36.2	38.8	39.3	40.5	44.4
	Session II					
1965	Area	5	2	3	4	1
	Sample size	567	977	880	928	342
	Mean weight	1.76	2.01	2.09	2.32	2.32
	Mean length	53.7	56.3	57.4	59.1	59.4

TABLE A5. (*Concluded*)

	Smallest					Largest
1966	Area	5	4	3	2	1
	Sample size	330	500	431	464	367
	Mean weight	1.45	1.99	2.04	2.17	2.20
	Mean length	50.0	55.9	56.3	57.7	58.2
1967	Area	5	4	3	2	1
	Sample size	500	500	500	500	500
	Mean weight	1.52	1.94	2.05	2.16	2.45
	Mean length	52.0	55.2	56.7	57.8	59.6
1970	Area	5	2	3	4	1
	Sample size	193	186	193	200	189
	Mean weight	1.52	1.64	1.69	1.72	2.11
	Mean length	50.8	53.0	53.0	53.5	56.8
1971	Area	3	4	1	2	5
	Sample size	202	235	200	179	180
	Mean weight	2.56	2.64	2.67	2.81	3.06
	Mean length	61.3	61.4	62.3	63.9	64.4
1972	Area	5	3	4	2	1
	Sample size	429	453	469	491	400
	Mean weight	2.09	2.21	2.43	2.40	2.59
	Mean length	55.2	57.7	59.1	59.2	60.8
1976	Area	2	4	3	5	1
	Sample size	430	1313	624	1229	1015
	Mean weight	2.44	2.15	2.13	2.31	2.50
	Mean length	57.0	57.5	57.5	58.3	59.5
				Session III		
1965	Area	5	4	3	2	1
	Sample size	357	398	352	463	130
	Mean weight	3.05	3.60	3.80	3.97	4.25
	Mean length	64.9	68.7	70.4	71.2	71.9
1966	Area	5	4	3	2	1
	Sample size	292	414	304	298	276
	Mean weight	2.20	2.85	3.08	3.14	3.37
	Mean length	62.7	64.4	65.2	66.7	67.5
1967	Area	5	3	4	1	2
	Sample size	266	359	311	159	181
	Mean weight	3.09	3.49	3.50	3.52	3.68
	Mean length	65.4	67.3	67.7	69.1	69.3
1970	Area	5	3	4	2	1
	Sample size	173	200	200	194	188
	Mean weight	2.42	3.47	3.30	3.53	3.56
	Mean length	60.8	68.2	68.4	68.4	68.5
1971	Area	1	2	4	3	5
	Sample size	201	156	179	200	165
	Mean weight	3.58	3.97	4.43	4.35	4.93
	Mean length	70.0	72.4	73.9	74.5	76.3
1972	Area	5	4	3	1	2
	Sample size	379	500	448	500	473
	Mean weight	3.45	4.03	4.06	4.13	4.20
	Mean length	66.8	69.9	70.0	70.8	71.0
1976	Area	1	2	3	4	5
	Sample size	823	899	741	1047	931
	Mean weight	3.80	3.91	4.18	4.16	4.09
	Mean length	68.6	69.4	71.2	71.4	71.5

TABLE A6. Mean lengths (mm) and weights (g) of underyearlings resident in the Main Lake during each fishing session. Mean lengths that are underlined are not significantly different from each other ($P > 0.05$).

			Session I				
Brood year	1967	1966	1965	1972	1970	1976	1971
Middate	July 11	July 17	July 11	July 8	July 13	July 18	July 4
Sample size	1239	1129	887	1072	615	3048	341
Mean weight	0.47	0.50	0.54	0.63	0.64	0.65	0.96
Mean length	35.6	36.0	36.8	37.3	37.5	38.9	44.1
			Session II				
Brood year	1970	1966	1967	1965	1976	1972	1971
Middate	Aug. 22	Sept. 7	Sept. 1	Aug. 28	Aug. 22	Sept. 2	Aug. 23
Sample size	494	1150	1283	3160	2842	925	477
Mean weight	1.71	2.04	2.06	2.10	2.27	2.38	2.74
Mean length	53.4	56.4	56.5	57.2	58.0	58.8	62.8
			Session III				
Brood year	1966	1970	1967	1965	1972	1976	1971
Middate	Oct. 15	Oct. 11	Oct. 14	Oct. 16	Oct. 8	Oct. 8	Oct. 12
Sample size	766	495	527	685	1177	2216	511
Mean weight	2.98	3.34	3.50	3.82	4.07	4.01	4.20
2Mean length	65.6	67.8	68.0	70.2	70.2	70.3	73.0

TABLE A7. Results of covariance analysis and the simultaneous test procedure on the regression coefficients of the length and weight relationships for each session and year. Slopes that are underlined are not significantly different ($P > 0.05$). $W = \log_{10}$ weight (g); $L = \log_{10}$ length (mm).

	SS	df	MS	F
		Session I		
Regressions	0.01894	6	0.00316	4.493***
Intercepts	0.15040	6	0.02507	35.679
Residual	0.22692	332	0.00070	
Total	0.39626	344		

Common regression line: $W = -5.580 + 3.277L$

Brood year	1971	1972	1976	1966	1965	1967	1970
Slope	2.948	3.089	3.273	3.365	3.376	3.425	3.497

	SS	df	MS	F
		Session II		
Regression	0.00577	6	0.00096	3.059**
Intercepts	0.04693	6	0.00782	24.891
Residual	0.11690	372	0.0031	
Total	0.16860	384		

Common regression line: $W = -4.218 + 2.792L$

Brood year	1976	1972	1965	1966	1967	1971	1970
Slope	2.437	2.571	2.792	2.803	2.815	2.867	2.885

	SS	df	MS	F
		Session III		
Regression	0.02257	6	0.00376	13.760***
Intercepts	0.07701	6	0.01283	46.949
Residual	0.09377	343	0.00027	
Total	0.19335	365		

Common regression line: $W = -4.358 + 3.005L$

Brood year	1972	1976	1965	1967	1970	1971	1966
Slope	2.359	2.378	2.632	2.800	3.044	3.056	3.238

A Cost-Benefit Method for Determining Optimum Closed Fishing Areas to Reduce the Trawl Catch of Prohibited Species[1]

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Red king crab (*Paralithodes camtschatica*), a prohibited species, are incidentally caught by United States trawl fisheries for yellowfin sole (*Limanda aspera*) and other groundfish in the eastern Bering Sea. To reduce this incidental catch, we propose a method for determining a king crab conservation zone where trawling would be prohibited. This method considers the gross revenue potentially gained by the yellowfin sole fishery and lost by the king crab fishery by allowing trawling in each of a number of equal-size areas. Utilizing exvessel prices and research survey estimates of species densities, areas are assigned relative values equal to the value of groundfish minus the value of king crab. By including all areas with negative relative values in the conservation zone, the potential gross revenue that could be obtained from the groundfish and king crab resource is maximized.

Des crabes royaux (*Paralithodes camtschatica*), une espèce prohibée, sont capturés de façon fortuite par des chalutiers des États-Unis qui pêchent la limande à nageoires jaunes (*Limanda aspera*) et d'autres poissons de fond dans la partie orientale de la mer de Béring. Afin de réduire ces prises fortuites, les auteurs suggèrent une méthode pour la délimitation d'une zone de protection du crabe royal où le chalutage serait défendu. Cette méthode tient compte des revenus bruts que pourrait produire la pêche de la limande à nageoires jaunes et des pertes brutes possibles pour la pêche du crabe royal si le chalutage était permis dans un certain nombre de zones de superficie égale. Des valeurs relatives, égales à la valeur du poisson de fond moins la valeur du crabe royal, sont assignées à chaque zone à partir des prix au bateau et des estimations de la densité des espèces. En groupant toutes les zones à la valeur relative négative dans la zone de protection, on maximise le revenu brut potentiel qui peut être obtenu des ressources de poisson de fond et de crabe royal.

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Incidental to their target species, trawl fisheries may also catch species that are the primary objects of other fisheries. If these incidental species are sufficiently valuable, they may be declared prohibited to trawlers and, as such, must be immediately returned to the sea. Such protection, however, may not reduce handling mortality sufficiently to prevent the directed fisheries from incurring a substantial loss. This situation may presently exist in the eastern Bering Sea (EBS) where a developing United States trawl fishery for yellowfin sole (*Limanda aspera*) incidentally catches red king crab (*Paralithodes camtschatica*), a relatively high-value species that supports a directed trap fishery (North Pacific Fishery Management Council 1981).

One way of reducing the loss of red king crab is to establish a conservation zone where bottom trawling would be prohibited. Although losses would be zero if this zone included the total range of red king crab in the EBS, such a conservation zone is so restrictive that it would limit future expansion of the yellowfin sole fishery. From the perspective of multispecies management, a more appropriate conservation zone is one that attempts to balance loss due to the incidental catch of red king crab against potential gain resulting from the catch of yellowfin sole and other groundfish.

In this paper we examine a technique for defining conservation zones, which considers the potential gains and losses in gross revenue that each of the fisheries would accrue if trawling were permitted. This technique assigns values to each of a number of equal-size areas based on exvessel prices and research survey estimates of the densities of red king crab, yellowfin sole, and other commercially important species. By combining these areas according to their values, a conservation zone is defined that is optimal in the sense of maximizing the gross revenue that could potentially be derived from the red king crab and groundfish resources.

Methods

Assigning Values to Areas

If gains and losses are measured in terms of gross revenue, trawling results in a gain to the yellowfin sole fishery equal to the exvessel value of the groundfish catch and also results in a loss to the king crab fishery equal to the exvessel value of the king crab that would have been harvested if they had not been incidentally caught. The difference between the value of the groundfish and the value of the incidentally caught king crab is thus a measure of the true value of allowing trawling in a given area.

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The value of each area is a function of catch and, therefore, a function of both the densities of the various species and the amount of fishing effort. The dependency on fishing effort complicates the problem of defining conservation zones because it is difficult to predict the redistribution of fishing effort that will occur should a conservation zone be established. This dependency can be removed, however, if value is expressed on a relative scale as value per unit of effort.

Relative values were based on the catch per unit effort (CPUE) of research vessels. Research catch data were chosen in preference to commercial catch data because they are available from a much larger area of the EBS than commercial data and because they are collected using standardized methods, thus providing more precise estimates of CPUE than commercial data. Research data were obtained from the Northwest and Alaska Fisheries Center (National Marine Fisheries Service) EBS stock assessment surveys conducted in 1979, 1980, and 1981. These surveys sampled crab and groundfish using a bottom trawl at the centers of a 38 × 38 km (20 × 20 nautical mile) grid covering the entire continental shelf of the EBS from nearshore to a depth of 200 m and from 61°N south to the Alaska Peninsula. The catch from each trawl sample was sorted by species and then weighed and counted. Commercial species were further separated by sex, and either total length in centimetres (fish) or carapace length in millimetres (king crab) was measured. Catches were standardized (catch per unit area trawled) before analysis.

To the yellowfin sole fishery, the value of a research trawl haul is equal to the sum of the weights of the commercially important species multiplied by their exvessel prices. The exvessel prices were assumed to be constant over the three years examined and equal to the 1980 prices (Fisher 1981). These prices were as follows: yellowfin sole, rock sole (*Lepidopsetta bilineata*), Alaska plaice (*Pleuronectes quadrituberculatus*), and flathead sole (*Hippoglossoides elassodon*) over 23 cm, $0.13·kg; Pacific cod (*Gadus macrocephalus*) over 35 cm, $0.20/kg; undersize food fishes and all other fishes suitable for fish meal, $0.03/kg.

To the red king crab fishery, the value of a research trawl haul is equal to the value of the male king crab (only males are harvested by the king crab fishery) that would have been harvested if they had not been incidentally caught. This value includes not only the expected harvest in the current fishing year but also the expected harvests in all future years that these crabs would have contributed to the king crab fishery. The expected harvest each year depends on the fishing mortality rate and the number of surviving crabs larger than the minimum legal size. To calculate the expected harvest, the size frequency distribution of the male crabs in each trawl haul was first converted to age frequency using size–age relationships (Table 1). The number of crabs in each age class surviving to future years was then calculated using estimates of natural and fishing mortality rates. If it is assumed that crabs become subject to harvest when they are 9 yr old (137 mm is the minimum commercial size), then the number of crabs (N) in year-class j that would have been alive when they were i yr old is

$$N_{ij} = N_{jj}\, e^{-\sum_{k=j}^{i-1} (M_k + F)}, \quad \begin{array}{ll} F = 0 & \text{when } k < 9; \\ F = 0.51 & \text{when } k \geqslant 9 \end{array}$$

where N_{jj} is the number of age j male crabs in the trawl haul, M_k is an age-specific instantaneous natural mortality rate (Table 1), and F is a constant instantaneous fishing mortality rate equal to 0.51 (North Pacific Fishery Management Council 1981). Since the king crab fishing season is short and within-season natural mortality is negligible, the expected harvest of year-class j crabs when they are i yr old is

$$C_{ij} = N_{ij} W_i (1 - e^{-F}), \quad \begin{array}{ll} F = 0 & \text{when } i < 9; \\ F = 0.51 & \text{when } i \geqslant 9 \end{array}$$

where W_i is the average weight of a male crab at age i (Table 1).

The value of crabs in a trawl haul is equal to the sum of the revenues that all year-classes would have generated, with future revenues discounted to present value. For a single year-class, assuming a maximum age of 14 yr (Balsiger 1974), the value of the expected harvest is

$$V_j = \sum_{i=j}^{14} C_{ij} P/(1 + D)^{i-j}$$

where V_j is the value of year-class j, P is the exvessel price, and D is an economic discount rate equal to 0.10. Since it is difficult to predict P in future years, P was assumed to be constant and equal to the exvessel price in the year of the survey ($2.11, $1.87, and $3.96/kg in 1979, 1980, and 1981, respectively). The total value of king crab is then equal to the sum of the present value of each of the 14 year-classes.

Incidentally caught female king crab were assumed to have zero value, both because females are not harvested by the king crab fishery and because the magnitude of the incidental catch is probably insufficient to affect future recruitment to the king crab stock.

TABLE 1. Size range, instantaneous natural mortality rate, and average weight of each of 14 age-classes of male red king crab (size ranges and weights from Balsiger (1974) and natural mortality rates from J. E. Reeves (Northwest and Alaska Fisheries Center, National Marine Fisheries Service, personal communication)).

Age	Size interval (mm)	Natural mortality rate	Weight (kg)
1	<23	0.50	—
2	24–48	0.40	—
3	49–69	0.30	—
4	70–86	0.20	—
5	87–102	0.13	—
6	103–117	0.12	—
7	118–130	0.08	—
8	131–137	0.08	—
9	138–145	0.11	2.34
10	146–149	0.23	2.55
11	150–152	0.50	2.78
12	153–154	0.57	2.90
13	155–156	0.61	3.02
14	>158	0.76	3.14

Determining an Optimum King Crab Conservation Zone

Assignment of areas to either the trawl fishing zone or the conservation zone was based on relative values: areas with positive or zero relative values were assigned to the trawl fishing zone and areas with negative relative values were assigned to the conservation zone. To demonstrate that this partitioning maximizes potential gross revenue, areas were first ranked according to relative value; then the cumulative value, summing from the most to the least value area, was plotted against rank (Fig. 1). Such plots show the combined value of all areas in the trawl fishing zone as each area is sequentially added. As areas of lesser value are added, cumulative value increases at a diminishing rate until the maximum is reached when an area of zero relative value is added. Further addition of areas reduces cumulative value below the maximum. Since the change in gross revenue that would be obtained by adding an area to the trawl fishing zone is equal to the product of its relative value and the amount of fishing effort expended, a partitioning that maximizes cumulative value also maximizes potential gross revenue. This is true because multiplication by fishing effort changes the magnitude but not the sign of the value of each area. Although the actual gross revenue that is obtained will depend on the distribution of fishing effort within the trawl fishing zone, the potential gross revenue will always be maximized if the trawl fishing zone contains only those areas with positive or zero relative values.

Although the areas comprising the conservation zones are fairly contiguous (Fig. 2), some areas included in the conservation zone are, because of sampling variability, surrounded by areas in the trawl fishing zone and some areas included in the trawl fishing zone are surrounded by areas in the conservation zone. To increase the unity of the conservation zones so that their geographical boundaries can be specified more easily, relative values were smoothed by averaging the values for each area with those of the four adjacent areas. The averaged relative values were then assigned to either the trawl fishing zone or conservation zone, as before. This smoothing eliminated most isolated areas and made the bounds of the conservation zones more regular (Fig. 2).

Forecasting Conservation Zones

Ideally, conservation zones should be based on stock density and price information collected immediately prior to the fishery, but this may not always be possible. In our case, the stock assessment survey occurs simultaneously with the yellowfin sole fishery; thus, data are available too late to determine an optimum conservation zone for the current fishing season. Conservation zones must, therefore, be forecast from historical data.

Two methods of forecasting were considered: dynamic and static. Dynamic forecasting consisted of applying the optimum conservation zone defined in one year to the fishery in the next succeeding year. Static forecasting consisted of defining a fixed conservation zone that is applied to the fisheries in a number of succeeding years. This fixed conservation zone was determined by averaging the smoothed relative values of each area over a baseline period (in our case over the three years 1979–81) and assigning those areas with negative relative values to the conservation zone (Fig. 3).

The relative predictive abilities of the two methods of forecasting were assessed by comparing the maximum total values of the forecasted conservation zones with those of the optimum conservation zones. Maximum total value was determined by summing the relative values of those areas outside a conservation zone. For an optimum conservation zone, this sum includes only those areas with positive relative values and is thus identical to maximum cumulative value. But, for a forecasted conservation zone, this sum may also include areas with negative relative values. The forecasted maximum total values for 1980, for example, were determined by summing the 1980 relative values of those areas outside the 1979 optimum conservation zone and by summing the 1980 relative values of those areas outside the fixed conservation zone.

Both methods of forecasting conservation zones resulted in maximum total values that were only slightly less than those of the optimum conservation zones (Table 2), but the static forecasts consistently resulted in larger maximum total values (averaging 95% of the optimum) than did the dynamic forecasts (averaging 88% of the optimum). The apparent greater predictive ability of the static forecasting method may simply be the result of not projecting the forecasts beyond the baseline years

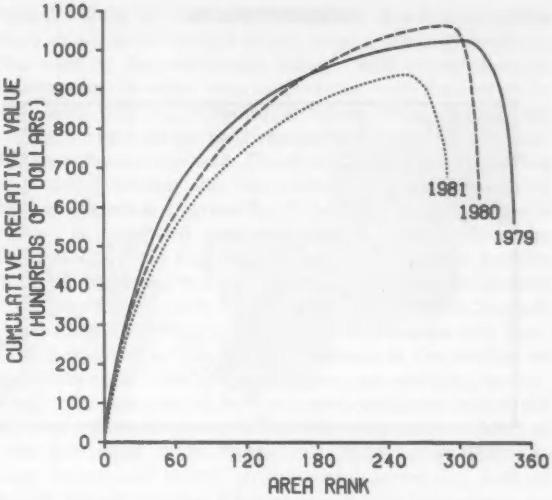

FIG. 1. Cumulative relative value and area rank. Cumulative value was calculated by ranking areas according to their relative values and then summing values from the most to the least valuable area. These plots show the change in total relative value after sequentially adding each area to the trawl fishing zone. Maximum total value is reached when an area of zero relative value is added. The optimum trawl fishing and conservation zones lay, respectively, to the left and to the right of the maximum.

TABLE 2. Maximum total value (dollars) of the optimum, dynamic forecasted, and static forecasted conservation zones in each of three years.

Year	Optimum max. total value	Dynamic forecast Max. total value	Dynamic forecast % of optimum	Static forecast Max. total value	Static forecast % of optimum
1979	967 552			937 730	97
1980	991 420	910 392	92	959 126	97
1981	878 202	739 503	84	800 539	92

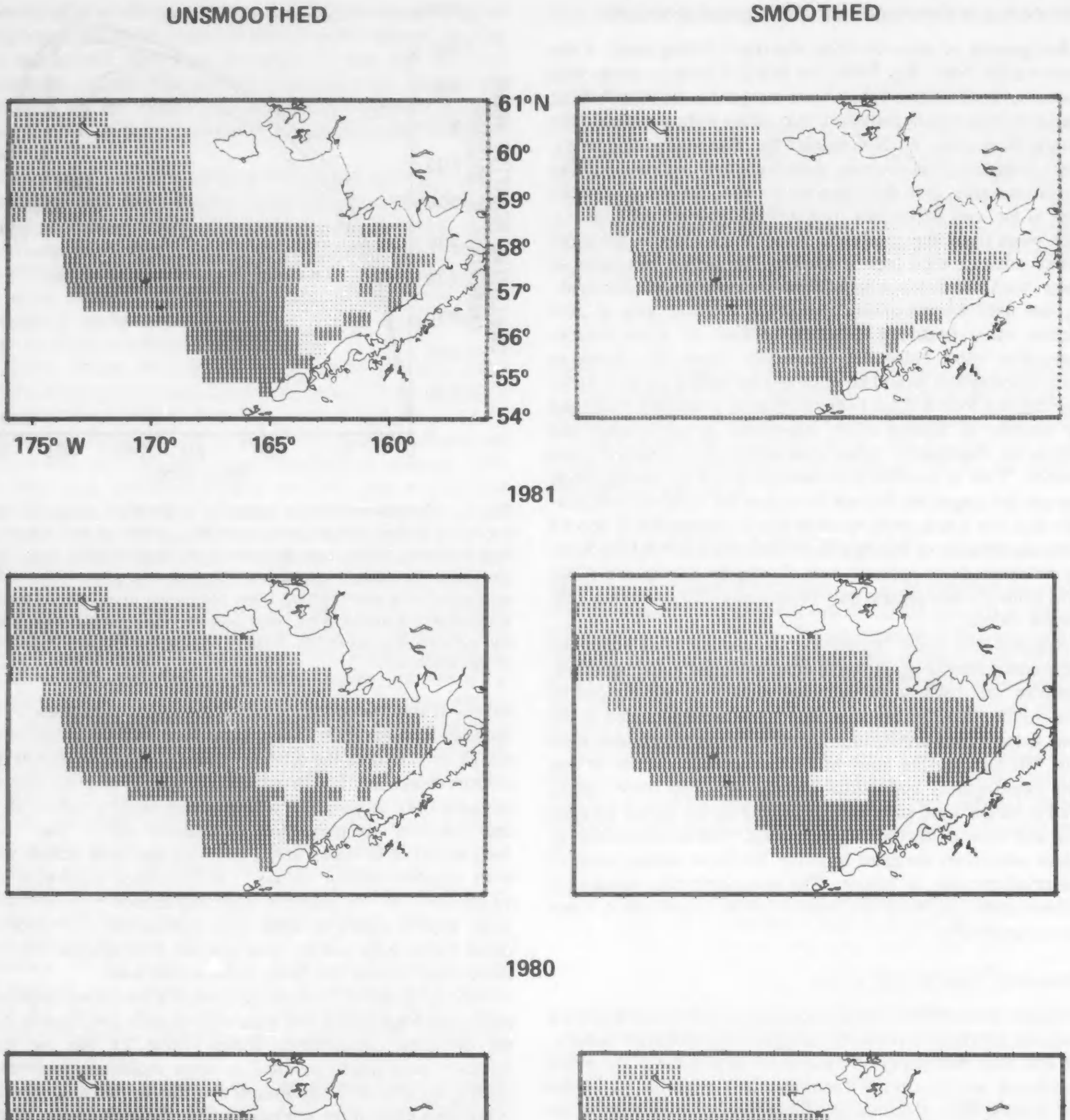
UNSMOOTHED
SMOOTHED
61°N
60°
59°
58°
57°
56°
55°
54°
175° W
170°
165°
160°
1981
1980
1979

FIG. 2. Locations of the trawl fishing zones (indicated by ×) and optimum red king crab conservation zones (indicated by ·) from 1979–81 before and after smoothing.

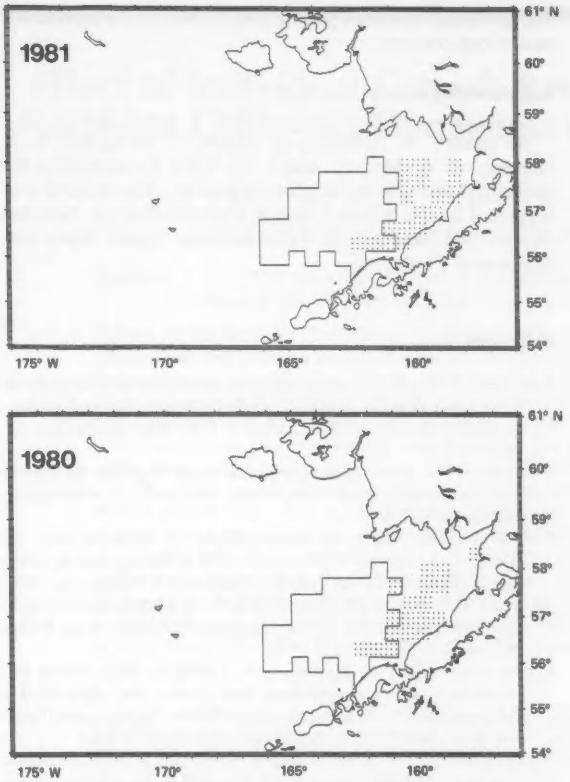

FIG. 3. Locations of the static forecasted king crab conservation zone (dark line) and the areas occupied by the yellowfin sole fleet during the 1980 and 1981 fishing seasons.

used to define the fixed conservation zone. If this projection were made, the static forecast would probably be similar to the dynamic forecast. In cases such as this, where maximum values do not differ greatly between forecasting methods, static forecasted zones are preferable because they do not need to be redefined each year and are more easily understood by fishermen.

Discussion

The proposed method for reducing the trawl catch of a prohibited species assigns areas to a trawl fishing zone or a conservation zone based on a measure of the true value of allowing trawling in each area. This measure is defined as the value of the trawl catch minus the value of the prohibited species, per unit of trawl effort. Areas having a positive value are assigned to the trawl fishing zone. Regardless of the distribution of fishing effort within the trawl fishing zone, such a partitioning maximizes the combined gross revenue that potentially could be obtained by both the trawl fishery and the fishery directed at the prohibited species. In addition, since trawling is only prohibited in those areas where the cost to the directed fishery exceeds the benefit to the trawl fishery, this partitioning is likely to be judged as equitable by both fisheries.

The specific case we chose to apply our method, the yellowfin sole fishery in the eastern Bering Sea, has features that simplified the problem of defining conservation zones but that may not apply to other situations. First, data were available from an extensive research survey using a gear type similar to that used by the commercial fishery. Such survey data are unnecessary, however, when commercial catch data are available from most of the potential fishing areas. Second, the interaction between the yellowfin sole fishery and the king crab fishery was only one way. The yellowfin sole fishery catches king crab, whereas the king crab fishery catches only a negligible amount of groundfish. In addition, the yellowfin sole fishery is prohibited from deriving any benefit from the incidentally caught king crab. When the trawl fishery benefits from the incidental catch or when both fisheries incidentally catch species important to each other, the problem becomes more complicated. Anderson (1975) and Marasco and Terry (1982) provided a more general treatment to the problem of incidental catch. Third, the catch of only one prohibited species, king crab, appeared to be significant enough to impact the directed fishery. However, losses due to incidental catches of other prohibited species, in particular, tanner crabs (*Chionoecetes bairdi*) and halibut (*Hippoglossus stenolepis*), both of which support directed fisheries, could have been easily included in the analysis.

The potential impact of a conservation zone on the yellowfin sole fishery is difficult to assess because the resulting redistribution of fishing effort depends not only on expected catch rates, which are imperfectly known by vessel operators, but also on factors such as the presence of obstructions to trawling and the distance to storm refuges. It is possible, however, to assess the worst case, that is, one in which the effort excluded from the conservation zone is not redistributed within the trawl fishing zone. Based on data collected by the United States fishery observer program (R. Nelson, National Marine Fisheries Service, 2725 Montlake Blvd. E., Seattle, WA, personal communication) for the 1980 and 1981 fishing seasons, we calculated three indices of the relative importance of the area within the proposed fixed conservation zone to the yellowfin sole fleet: (1) percent of total area fished (Fig. 3), (2) percent of total effort (number of trawl hauls), and (3) percent of total catch. These are tabulated below:

	1980	1981
% of area fished	28	16
% of total effort	15	20
% of total catch	18	24

If there was no redistribution of effort in these two years, the catch would have been reduced by as much as 24%; however, any redistribution of effort would have substantially reduced this loss.

Since research data were used as a proxy for commercial catch data in our analysis, the assignment of areas to either the trawl fishing zone or the conservation zone is only valid to the extent that the two types of data are equivalent. Although both the time of the research survey (May–August) and the fishing gear used (Pereyra et al. 1976) were similar to the yellowfin sole fishery (Fisher 1981), it is possible that the catches differ because research vessels trawl at predetermined locations, whereas commercial vessels trawl in areas of high groundfish abundance. Because the assignment of areas was based on the difference between the value of fish and the value of king crab, it is not the difference in catch rates that is important but the difference in the relative proportion of king crab to fish in the catches. To determine if such a difference existed, the 1981 average species proportions (weight of king crab divided by weight of groundfish) within 1° longitude and 0.5° latitude statistical areas were compared. These proportions were not found to be significantly different (Wilcoxon signed rank statistic = 18, df = 10, two-tail probability > 0.20).

Although no difference in species proportion was detected, such a difference could develop in the event that a conservation zone were established. Trawl fishers might alter their fishing techniques to catch fewer crabs if by doing so they would gain access to a larger fishing area. Provided that the catch rates of fish are not also reduced, such changes should be encouraged because potential gross revenue would be increased. Incentive for this could be provided if the species proportions of the research catches used to define conservation zones were routinely adjusted to reflect the species proportions of the commercial catches.

Our method for defining conservation zones was based on the optimality criterion of maximum revenue; but maximum profit would have been a better optimality criterion because profit is a better measure of net benefit. We chose our approach because we were unable to devise a profit-maximizing allocation scheme that was independent of the distribution of effort. Such an allocation scheme would require estimates of profit and, therefore, estimates of variable and fixed operating costs to be expressed on a per unit of effort basis. The crux is specifying fixed costs per unit of effort. If, however, it is assumed that (1) the increase in the directed catch of king crab resulting from the establishment of a conservation zone is insufficient to affect either the exvessel price or cost of harvesting and (2) the costs of harvesting either king crab or groundfish do not differ among areas, then a conservation zone that maximizes gross revenue will be approximately equal to a conservation zone that maximizes profit.

Other methods of controlling incidental catch, such as gear restrictions or taxation (Marasco and Terry 1982), may be more effective than closed fishing areas in terms of increased profit. The advantage of closed fishing areas, however, is the relative ease of enforcement.

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Effect of Individual Growth Rates on Expected Behavior of the Northern California Dungeness Crab (*Cancer magister*) Fishery

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Botsford, L. W. 1984. Effect of individual growth rates on expected behavior of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 41: 99–107.

Cycles in the northern California Dungeness crab (*Cancer magister*) fishery may be caused by density-dependent recruitment or a cyclic environmental variable. Investigation of these potential causes requires knowledge of the age(s) at which crabs enter the fishery. Behavior of this fishery has previously been analyzed using mathematical models that include density-dependent recruitment and describe changes in age structure with time. From data available on the northern California crab population and a review of previous studies elsewhere it appears that a single year-class of crabs enters this fishery over several years rather than in one year as described by models with only age structure. The realism of models of this fishery can therefore be increased by including size structure. Behavior of size-specific models is in general different from that of age-specific models. However, it is shown here that an effective survival rate can be derived from a size-specific model that enables interpretation as an age-specific model. This is used to demonstrate that inclusion of size dispersion in a population model increases stability, but if the mean age of the population is not changed, it will not substantially change the period of cycles. Because the growth pattern developed here changes the mean age of entry into the fishery it results in cycles with a longer period than determined in previous analyses. With regard to environmental causes, this growth pattern implies time lags of 4 and 5yr between an environmental factor affecting recruitment and its effect on the catch record.

La nature cyclique de la pêche du dormeur du Pacifique en Californie septentrionale (*Cancer magister*) peut être le résultat d'un recrutement lié à la densité ou d'une variable environnementale cyclique. Une étude de ces causes potentielles requiert une connaissance de l'âge des crabes au moment où ils atteignent une taille exploitable. On a déjà analysé le comportement de cette pêche à l'aide de modèles mathématiques qui couvrent le recrutement lié à la densité et décrivent les changements de la composition par âge en fonction du temps. Selon les données disponibles sur la population de crabes de la Californie septentrionale et un examen des études précédentes réalisées ailleurs, il semble qu'une seule classe d'âge se joint à la population vulnérable sur une période de plusieurs années plutôt qu'au cours d'une seule année comme le décrivent les modèles ne comprenant que la composition par âge. On peut donc accroître le réalisme des modèles de cette pêche en y incluant la composition par taille. En général, le comportement des modèles de tailles diffère de celui des modèles d'âges. Le présent rapport montre qu'on peut dériver un facteur de survie efficace à partir d'un modèle de tailles qui permet de tirer une interprétation comme un modèle d'âges. On utilise ce fait pour démontrer que l'utilisation de la répartition des tailles dans un modèle de population en augmente la stabilité; toutefois, si l'âge moyen de la population n'est pas changé, ce facteur ne modifiera pas considérablement la période des cycles. Parce que le régime de croissance élaboré dans le présent rapport modifie l'âge moyen où le crabe devient vulnérable à la pêche, il en résulte des cycles de périodes plus longues que celles déterminées par des analyses précédentes. En fonction des facteurs environnementaux, ce régime de croissance suppose des décalages de quatre et cinq ans entre, d'une part, l'effet d'un facteur environnemental sur le recrutement et, d'autre part, l'incidence de ce facteur sur les prises.

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There are several potential classes of causes of the observed cycles in the northern California Dungeness crab (*Cancer magister*) population. The possibility of a predator–prey mechanism with man as the predator has been discounted (Botsford et al. 1983) and investigations of environmental influences continue (for examples of these see Botsford and Wickham 1975; Wild 1980). A third possible cause of the observed cycles in abundance and catch in the northern California fishery is density-dependent recruitment.

Botsford and Wickham (1978) proposed this type of mechanism and analyzed stability of a population model that was age-specific (i.e. it kept track of the number of animals at each age) and included density-dependent recruitment. They showed that (1) the period of the cycles produced was approximately twice the time between the age at which density-dependent recruitment affects young individuals and the mean age at which adult individuals affect recruitment in a density-dependent fashion and (2) for cycles to occur, recruitment survival must change at a certain rate as adult population size changes. They proposed that these derived characteristics be used in conjunction with field data from potential density-dependent recruitment mechanisms to determine which mechanism(s) demonstrated the characteristics necessary to cause cycles. They advanced two potential causal mechanisms that had been shown to be present in this population: cannibalism and an egg-predator worm whose density (and effective egg mortality) could depend on female crab density. Data being collected on cannibalism and the egg-predator worm will be compared with derived stability conditions (i.e. period of cycles and rate of change of recruitment survival).

Use of the above stability results to reject proposed hypothetical causes of the cycles requires confidence in the assumptions on which the model is based. If one of them is not true, a negative outcome of a comparison of model predictions with observed behavior can lead to erroneous rejection of a hypothesis. In that case a part of the model other than the primary hypothesis being tested is responsible for the disparity.

Investigation of possible environmental causes of the cycles also requires an accurate model of crab life history. These investigations usually involve examination of the statistical relationship between environmental variables and the catch or abundance record. The most likely age of influence of oceanographic environmental variables on the crab would be the planktonic larval phase. Therefore, knowledge of growth rate and survival is necessary to determine the time lag(s) at which a high correlation would be expected.

The work described here is part of a systematic effort to increase the realism of the description of the Dungeness crab population so that it can confidently be used to evaluate whether proposed density-dependent and environmental mechanisms are causing the cycles. We describe here the changes in expected population behavior brought about by including a more realistic description of individual growth in the model.

There were several departures from reality in the models used in previous stability analyses. Methot and Botsford (1982) showed that harvest rate was not a high constant factor as had been previously assumed but rather varied in response to abundance. Botsford et al. (1983) analyzed the implications of the time-lagged response of effort to changes in abundance in this fishery. The effect of lagged effort on behavior of a model with density-dependent recruitment was to make the population less stable and to cause the period of the cycles to be longer than the period of those produced by a model with constant effort.

A second departure from reality stems from the fact that a model that has only age structure was used. In an age-specific model each age-class is either in the fishery or is not in the fishery. In reality, however, availability to the fishery depends on size rather than age. Because of the distribution of sizes within an age-class, some members of an age-class may become greater than legal size (159 mm carapace width) several years before others in that age-class. The effect of including realistic growth in a population model with density-dependent recruitment is described here.

Size-Specific Models: Analytical Expectations

To represent the effect of a size-selective fishery on the size distribution of each age-class we must use a size-specific model. There are two basic types of size-specific models: (1) the continuity equation with size as one of the independent variables in the density function (Sinko and Streifer 1967; Botsford 1978) and (2) a diffusion equation, also with size as one of the independent variables in the density function (Weiss 1968). The choice between these depends basically on the nature of the growth mechanism that leads to increase in mean and dispersion in the size distribution. In the former, growth of an individual is a deterministic process, while in the latter it is a random Markov process. Since we are interested here in the aspects of growth over time that arise from a continuous, deterministic growth of individuals rather than the random fluctuation about that growth, the continuity equation is used (see Botsford 1978 for further discussion of the choice between the continuity and the diffusion equation). Also, the discrete nature of crustacean growth (i.e. that crabs grow by molting) is not explicitly considered here. By the time that crabs are near legal size, lack of molt synchrony and other factors lead to a size distribution that is a smooth function rather than a collection of different distinct modes corresponding to different molt stages.

The continuity equation that describes the change in time of the number of animals of size m at age a, $n(m, a)dm$, can be written

$$(1) \quad \frac{\partial n(m, a)}{\partial a} = -\frac{\partial}{\partial m}[g(m, a)n(m, a)] - D(m, a)n(m, a)$$

in which $g(m, a)$ = the individual growth rate at size m, age a, and $D(m, a)$ = the instantaneous mortality rate at size m, age a. This equation as written applies to a single cohort. It can be solved by integrating along characteristic lines (Appendix A).

Dispersion of the size distribution can arise from four different types of mechanisms. first, it can be present in the initial conditions. Either individuals being reproduced at a range of different sizes or reproduction occurring over a nonzero time period will lead to this type of mechanism. This effect is probably small in terms of absolute size differences but will be enhanced by the second mechanism that influences size dispersion, nonlinear growth. The first term on the right-hand size of equation 1 can be written as

$$(2) \quad -\frac{\partial}{\partial m}[g(m, a)n(m, a)] = -g(m, a)\frac{\partial}{\partial m}n(m, a) - n(m, a)\frac{\partial}{\partial m}g(m, a).$$

The first term is analogous to the partial derivative with respect to age of the age density in the well-known age-specific continuity equation of McKendrick (1926) and Von Foerster (1959). It describes the rate at which animals grow into size m (or age a). The second term, however, is not present in the age-specific equation. It describes the tendency of an age distribution to "spread out" because of a nonlinear growth function (e.g. if growth rate is increasing with size, an individual that is slightly smaller than another becomes increasingly smaller than that individual as time goes on because it is of a size that has a lower growth rate). Note that if growth (size versus time) is linear, $g(m, a)$ is constant with m and the second term is zero. The third mechanism is a distribution of growth rates. If individuals have inherently different growth rates the size distribution can increase in width. The fourth mechanism is random variation of growth rate of each individual over time. This mechanism leads to the diffusion equation description mentioned earlier (Weiss 1968) and is assumed not to be important here.

For the latter two deterministic mechanisms we can convert the size-specific model to an equivalent age-specific model and evaluate the expected influence of size structure on population stability and period of the cycles produced. We can express the age-specific fraction surviving from age zero to age a in the absence of fishing, $\sigma(a)$, as

$$(3) \quad \sigma(a) = \int_{m_0}^{\infty} \tilde{n}(m, a)dm$$

where m_0 = the size at which individuals are recruited into the population and

$$\tilde{n}(m, a) = n(m, a) / \int_{m_0}^{\infty} n(m, 0)dm.$$

We assume that we can solve for the function $n(m, a)$ (hence $\tilde{n}(m, a)$) that arises from natural growth and mortality and then examine the effects of fishing. From Appendix A, if we add a constant fishing mortality rate E for sizes $m > m_1$ we can express the normalized size density with fishing, $\tilde{n}_f$, as

$$\begin{aligned}(4) \quad \tilde{n}_f(m, a) &= \tilde{n}(m, a) \exp\left[-E \int_{m_1}^{\infty} \frac{dm'}{g(m')}\right] & m \geqslant m_1 \\ &= \tilde{n}(m, a) & m < m_1.\end{aligned}$$

Using this in equation 3 instead of $\tilde{n}(m, a)$ yields the survival function with fishing

$$(5) \quad \sigma_f(a) = \int_{m_0}^{\infty} \tilde{n}(m, a)F(m)dm$$

in which

$$\begin{aligned}F(m) &= \exp\left[-E \int_{m_1}^{\infty} \frac{dm'}{g(m')} dm'\right] & m \geqslant m_1 \\ &= 1 & m < m_1.\end{aligned}$$

As can be seen in Fig. 1, if the size distribution has zero width, $\sigma_f(a)$ merely reflects specific values of the fishing mortality function multiplied by natural survival. This corresponds to the case represented by the previous age-specific models. If the size distribution has nonzero width, however, $\sigma_f(a)$ is a "smeared" version of the fishing survival function. The survival function begins to decline at an earlier age and remains positive to a later age than a zero-width distribution.

Botsford and Wickham (1978) showed that the stability (propensity to cycle) of this population model and the period of the cycles depend on the age structure (i.e. on the product of survival to age a, $\sigma(a)$, and a function that reflects the relative influence of an animal at age a on density-dependent recruitment). A broad, flat age structure correspond to a more stable population and a narrow, peaked age structure corresponded to a less stable population. the period of the cycles was approximately twice the mean age of the age structure. Hence, as the addition of a size distribution "smears" the survival function it would also "smear" the age structure causing it to become less peaked. One would therefore expect the population to become more stable. Since the addition of size structure to the model causes the effective survival function to decline at an earlier age and increase at a later age, these two changes could compensate for each other, leaving the mean age constant. To the extent that this happens, the period of the cycles would not be expected to change.

Dungeness Crab Growth

Since crustaceans increase in size in discrete steps through the process of ecdysis and retain no hard parts that might have annual growth marks, their individual growth rates are difficult to determine (see Botsford 1984 for a review of methods used to quantitatively describe crustacean growth). They can be tagged with tags that are retained through the molt and also held in the laboratory or in live wells to determine the size increment per molt. However, the additional information needed to completely determine growth rate, the time increment between molts, is difficult to obtain. A second method of determining growth rate is by following size modes that correspond to age-classes through plots of size distribution for several sequential years. Both types of data have been collected for Dungeness crabs.

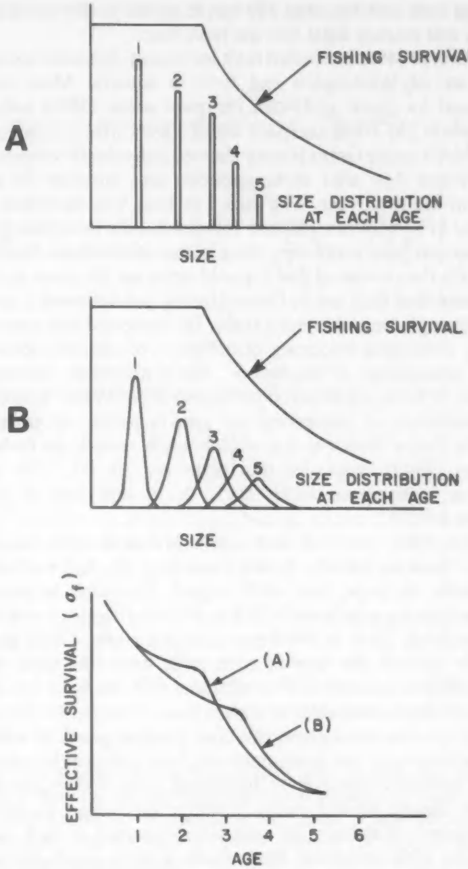

FIG. 1. Effect of nonzero width size distribution on the effective survival rate. (A) Zero-width or age-specific case; (B) nonzero-width case. Effective survival at each age is the integral over the product of the size distribution at that age and the fishing survival. Size dispersion distorts the effective survival function.

MacKay and Weymouth (1935) recorded molt increments from crabs molting in captivity and under natural conditions in Boundary Bay, British Columbia, and near San Francisco, California. The average molt increment in males decreased from 40% at 50 mm carapace width to 15% at 135 mm carapace width. Of the more than 1000 crabs tagged by them, there was only one case of a crab having gone more than 1 yr without molting. From this they concluded that a single annual molt was likely. From their observations of size distribution in the first 3 yr (10–20, 40–70 and 100–120 mm for shortly after metamorphosis 1, 2, and 3 yr later, respectively) and molting data they constructed a model of crab growth. From this model the average male crab becomes 150 mm in his 6th yr after metamorphosis and reaches legal size the next year.

Cleaver (1949) determined molt increments for crabs taken in the state of Washington and held in aquaria. Male crabs increased by 3 mm at 10 mm carapace width (30%) and by 24.0 mm at 155.0 mm carapace width (16%). Size distributions from trawls inside Grays Harbor showed individuals between 30 and 70 mm 1 yr after metamorphosis and between 80 and 120 mm the next year. The size 1 yr later was identified by Cleaver to be between 140 and 160 mm but the transition from the previous year is not very clear in the intermediate distributions. He then assumed that 3-yr-old crabs are the same size in the ocean that they are in Grays Harbor and followed a year-class through the commercial traps. He supported this assumption by comparing frequency distributions of cast exoskeletons inside and outside of the harbor. The distributions shown in support of this assumption do not appear to be similar. Based on this procedure of connecting the growth pattern of younger crabs in Grays Harbor to that of older crabs outside the harbor, Cleaver (1949) concluded that crabs are 30, 95, 150, and 175 mm in carapace width at 1, 2, 3, and 4 yr of age, respectively.

Butler (1961) collected molt increment data on crabs from the Queen Charlotte Islands, British Columbia, that had molted in live wells, in traps, and while tagged. The molt increment declined from approximately 28% at 80.0 mm carapace width to approximately 18% at 160.0 mm carapace width. Using these data he derived the size at each molt stage and used that relationship to interpret size distributions from the field. His size distributions show a peak that moves from 20 mm to 30–80 mm almost 1 yr after metamorphosis. Size distributions from which sizes at later ages are determined are from different locations. These generally show crabs distributed from 100 to 200 mm with no clearly defined modes between these sizes. Based on comparisons of these plots with sizes expected at each molt (from the molt increment data), Butler (1961) concluded that males are approximately 120 mm at 2 yr, 148 mm at 3 yr, and 175 mm at 4 yr (from metamorphosis).

Poole (1965) collected molt increment data on crabs from Bodega Bay that had molted in traps, in tanks shortly after capture, and while tagged in the ocean. Size increments declined from approximately 30% at 20 mm carapace width to approximately 15% at 160 mm carapace width. Poole (1965) was successful in following a good year-class through several years of development. He followed the 1961 year-class for several years after June 1961 at which time it ranged from 5 to 18 mm in carapace width. One year after metamorphosis the year-class ranged from 70 to 110 mm. Although the size distribution of the single age-class eventually became difficult to identify he concluded that some crabs enter the fishery at 2.5 yr after metamorphosis, most enter at 3.5 yr, and the remainder at 4.5 and possibly 5.5 yr after settlement. Poole (1965) noted that growth of this year-class was faster than growth of crabs in Washington and Oregon, appeared to be faster than the 1962 year-class, and was faster than projected by molt increment data.

The growth data most pertinent here are crab size distributions from trawl samples taken on cruises conducted by the California Department of Fish and Game in Northern California each November (before the fishing season) from 1958 to 1975. In two instances these show a large year-class of young crabs that can be followed through several years.

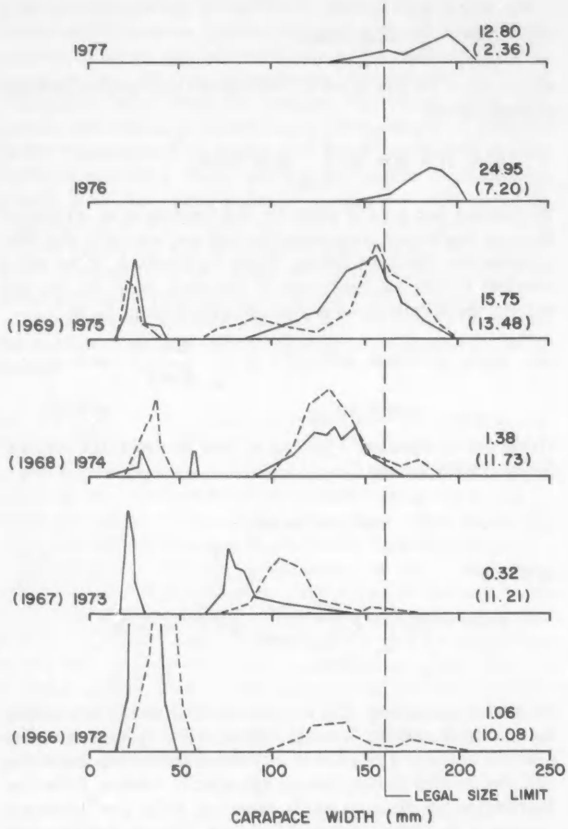

FIG. 2. Size distribution from November cruises by the California Department of Fish and Game for 1972–77 (solid curve) and 1966–69 (broken curve). Total catch in the commercial fishery for the fishing season following the sample (December–June) is listed to the right of each plot (1966–69 in parentheses). Data for 1976 and 1977 were collected using commercial traps, hence are biased to sizes greater than 150 mm. Data for earlier years were collected by trawl. Because of changes in sampling procedures, vertical scales are not necessarily the same for each year.

As shown in Fig. 2, samples taken in 1966–69 clearly show the 1966 age-class (data obtained from B. Hammer, California Department of Fish and Game, 411 Burgess Dr., Menlo Park, CA 94025). They indicate a small contribution at age 2.5 (age from metamorphosis) and slightly less than one half of the cohort in the fishery at age 3.5. There were no trawl samples the following year but it appears that the second half would have entered the fishery in that year.

Also shown in Fig. 2 is the 1972 year-class in samples taken with a trawl and commercial traps with closed escape ports each November through 1975 and sampling only with commercial traps with closed escape ports for 2 yr thereafter (data from R. Warner, California Department of Fish and Game, 619 2nd St., Eureka, CA 95501). Traps are ineffective for small crabs, and trawls may be less effective for larger crabs, but traps and trawls appear to have similar size distributions for crabs larger than about 150 mm. From these data, the 1972 year-class appears to contribute a minor amount to the fishery at age 2.5 (note that the catch for that year is only 1.38 × 10^6 kg) and then contributes to the catch over the next 2 yr and possibly the third. Interpretation

TABLE 1. Description of growth of Dungeness crabs used in the model from which stability results are derived. The effect of fishing is not included. One year of age is taken to be the November after hatching the previous winter. All sizes are sizes in November.

Age (yr)	Carapace width (mm)			
	Males		Females	
	Mean	SD	Mean	SD
1	25	3.0	25	3.0
2	90	10.8	90	10.8
3	130	15.6	120	14.4
4	158	19.0	136	16.3
5	186	22.3	152	18.2
6	214	25.7	152	18.2
≥7	214	25.7	152	18.2

of these data is complicated by the fact that the 1973 year-class cannot be differentiated from the 1972 year-class in later years.

Because the contribution of the 1972 year-class beyond age 4.5 yr cannot be clearly distinguished, I have adopted a baseline growth pattern that approximates that of the 1966 year-class and the 1972 year-class without crabs entering the fishery beyond age 4.5 yr (Table 1). size of males in the first 3 yr is a rough estimate taken from modes of the size distribution in Fig. 2. for the following 3 yr I assume that there is one molt per year at an increment of 28 mm (19% at 150 mm). This leads to a small number entering the fishery at 2.5 yr and the remainder of the year class entering in equal amounts at ages 3.5 and 4.5. Female growth rates are taken from the modes in Poole (1965) and the California Department of Fish and Game data for the first 3 yr of growth with a constant increment of 16 mm/yr for the following 2 yr. To evaluate the effect of crabs entering the fishery at age 5.5 yr, model behavior is also examined for a growth pattern that includes crabs entering the fishery at ages 3.5, 4.5, and 5.5 in the approximate ratio of 1:2:1 (with a small amount entering at age 2.5).

For comparison with Fig. 2, the size distributions that result from these two assumed growth patterns are shown in Fig. 3. For this example, recruitment rate is set to a low, constant level for all years except 1972 when a large recruitment pulse is introduced. The harvest rate is constant at 0.6.

Simulation Results

To directly determine the effect of a more realistic description of growth on stability and the period of cycles, simulations were run of a model similar to that described in Botsford and Wickham (1978) and Botsford et al. (1983) except for a difference in the growth model. Since the actual mechanisms of size dispersion are not known, a phenomenological description was used. Each age-class had the mean sizes and widths shown in Table 1. Individuals at one point in the size distribution at one age moved to the corresponding point in that distribution at the next age (they remain the same distance from the mean in units of the standard deviation) unless removed by fishing or natural mortality (e.g. see Fig. 3).

The natural survival function $\sigma(a)$ is the same as the baseline case in Botsford and Wickham (1978). However, since the weighting function that describes the relative effect of older individuals on density-dependent recruitment was assumed there to be individual weight to the 0.8 power, it changes with the new growth rates. The function $\sigma_f(a)$ as computed from equation 5 is shown in Fig. 4 as the degree of size dispersion changes from a zero-width distribution to a size distribution with a ratio of standard deviation to mean (coefficient of variation, c.v.) of 0.24.

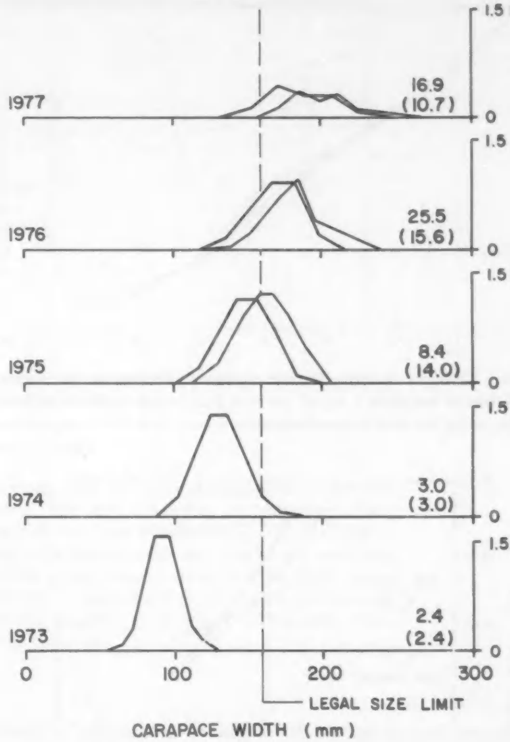

FIG. 3. Size distribution from simulation for comparison with data in Fig. 1. Both the baseline interpretation of growth (i.e. faster growth) and the alternative interpretation are shown. Catch for each year (assuming a harvest rate of 0.6) is listed to the right of each plot (baseline in parentheses).

The influence of size dispersion on stability of the model and period of the cycles in a harvested population is shown in Fig. 5. For all cases shown, both the stable point K' (the slope of the stock-recruitment curve at which the population becomes unstable) and the period of the cycles decline with increased harvest rate. This result is commensurate with the notion that stability declines as the age structure becomes narrower and period decreases as the mean age decreases. The stable point K' and period of cycles for the former age-specific model are shown for reference. As the model is changed to include the new baseline growth rate and size dispersion (i.e. individuals entering the fishery at age 3.5 and 4.5 rather than complete recruitment at age 3.5), the period of cycles increases and stability decreases at lower harvest rates and increases at higher harvest rates.

Results for the alternative growth model (not shown) were similar but also demonstrate an additional feature. For that model there is no change in period as dispersion is added (recruitment at ages 3.5, 4.5, and 5.5) to the mean growth rate

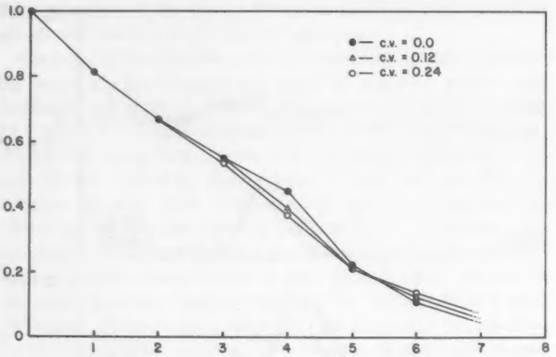

FIG. 4. Changes in the effective mortality function as the width (coefficient of variation c.v.) of the size distribution varies from 0.0 to 0.24, using the slower growth rate.

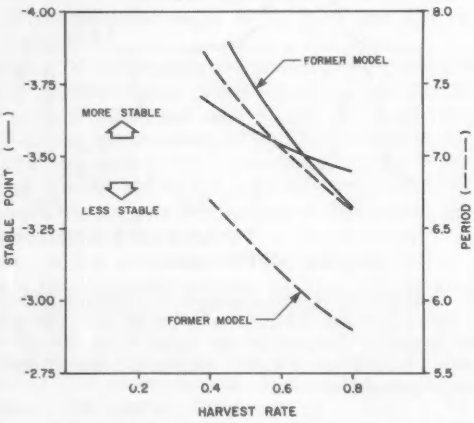

FIG. 5. Changes in stable point and period as harvest rate changes, for the former model (all recruited at age 3.5, c.v. = 0.0) and the baseline growth interpretation (recruited at ages 3.5 and 4.5, c.v. = 0.12).

(recruitment at age 4.5 only). This is commensurate with Fig. 3 in which size dispersion causes a change in shape of the age structure but little change in mean age; hence, the stable point may change but the period will not. Addition of dispersion causes the period to change in the baseline growth model because dispersion causes increased recruitment at higher ages, hence an increase in the mean age of the population.

Since the stability of this type of model is affected both by size dispersion (as shown here) and a lagged response of effort to abundance (Botsford et al. 1983), the effect of both together must be known to assess the real population. Stability and period of cycles produced by a model that includes size distribution and the lagged effort model presented in Botsford et al. (1983) are shown in Fig. 6. In the latter model the harvest rate is nominally 0.6 but depends on previous abundance. The degree of dependence of harvest rate on previous years increases with the parameter *U* (abscissa in Fig. 6). The effect of increasing *U* on the age structure model used in Botsford et al. (1983) was to increase the period of cycles and to initially decrease stability after which it increased (Fig. 6). This general behavior holds when the baseline growth rate is added to the model. However, although the stability point is similar at all values of *U*, the period is greater than in the former model. Results for the alternative interpretation of growth rate (not shown) are similar except that the population is more stable for all values of *U*.

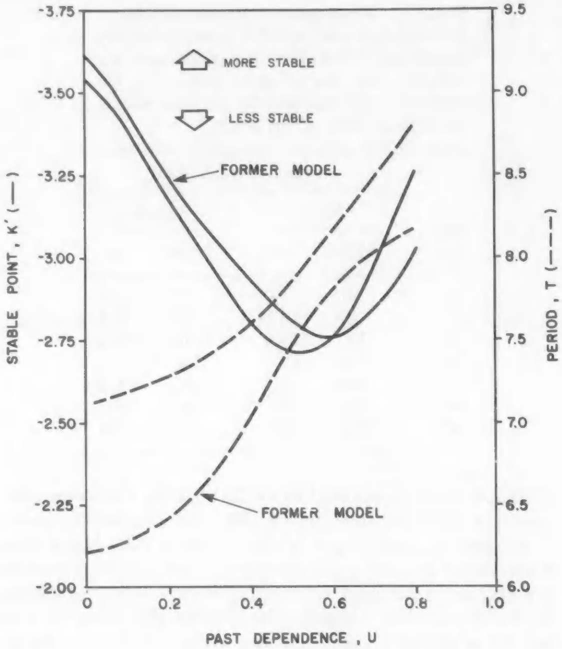

FIG. 6. Changes in the stable point and period of the cycles as the dependence of effort on previous catch is increased, for both the former model and the baseline growth interpretation.

Discussion

The addition of size structure to age-specific population models with density-dependent recruitment is shown here to increase stability with little change in the period of population cycles. Since these results are based on an interpretation of equation 5 and typical behavior observed in previous results (i.e. the influence of the shape of the age structure on dynamic behavior), they are not necessarily general but rather depend on the specific population. The derivation of effective survival (equation 5) would hold for all models of this nature, but the interpretation of the influence of age structure on stability, while it has been referred to by others, has only been shown analytically to be true for a simple case (Botsford and Wickham 1978). The period of the cycles is not likely to change with the addition of size structure if the decrease in effective survival at younger ages is compensated for by the increase in survival at older ages in such a way that the mean age of the population age structure remains constant.

The growth description used in the simulation is not completely realistic in that the process of growth by ecdysis is not explicitly included. If growth at ages at which individuals are in the fishery consists of a single molt between the same sizes each year, as is thought to be the case, then not including these details will have no effect on the results.

The simulation results depend on the growth rates used.

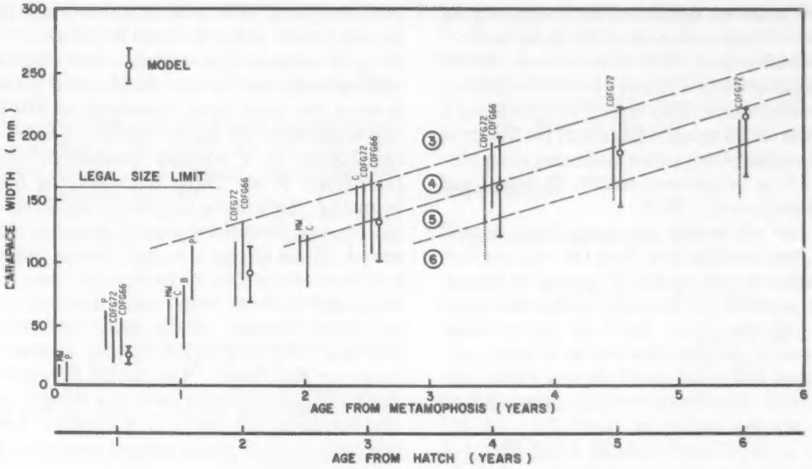

FIG. 7. Summary of male Dungeness crab data. Vertical lines are size distributions of known age from specific references (B = Butler 1961; C = Cleaver 1949; MW = MacKay and Weymouth 1935; P = Poole 1965; CDFG72 = California Department of Fish and Game samples (1972–77); CDFG66 = California Department of Fish and Game samples (1966–69)). Circles with error bars are the mean size and twice the standard deviations used here in the baseline growth interpretation (with the effects of the fishery included in later years). Circled numbers indicate the age (from hatching) at which a crab between the two increasing lines will enter the California fishery if he grows at 28 mm/yr. Dotted parts of the CDFG72 line indicate possible involvement of a second age-class.

However, there is little difference between the stability results obtained here for the two possible interpretations of growth rate. Also, since the 1972 age-class was extremely large, growth, if density dependent, may have been unusually slow. The effects of density-dependent growth rate have not been investigated.

The growth rates used here are somewhat slower than those determined by Cleaver (1949). His result was based on following size modes in Grays Harbor through the 3rd yr of age and then assuming that growth rate in the harbor was the same as that outside. His conclusion that the major contribution to the fishery would occur at 3.5 yr of age (years from metamorphosis) depends critically on that assumption. There is some evidence that juvenile Dungeness crabs grow more rapidly in bays and estuaries than in the open ocean. Orcutt (1977) found that crabs in San Francisco Bay reached 110 mm 1 yr after settlement. In Gotshall's (1978) size distribution the mode is approximately 80 mm in November in Humboldt Bay and does not change much in the following 6 mo. These values are in contrast with the mode in Fig. 2 at approximately 30 mm in November, 6 mo after settlement.

Comparison with Butler's (1961) growth rates is difficult because metamorphosis occurs in late summer in British Columbia rather than late spring as in California. His growth profile reaches 148 mm 3.0 yr after metamorphosis, while the one in Table 1 reaches 158 mm 3.5 yr after metamorphosis (Table 1).

Poole's (1965) data show a slightly larger size at 1 yr than those used here (30–60 versus 20–50 mm) and are also larger after the second summer. Further comparisons are difficult because later samples are taken by commercial crab traps rather than trawls.

This cursory review of the growth studies of this crab reveals little agreement although this is partially caused by problems such as differences in month of metamorphosis, month of sampling, and whether reared in bays or estuaries. Typically, size modes can be followed through the first couple of years, but sizes at later ages have not been confidently identified. Studies in which young crabs of known age are tagged and followed through the next several years are required for better definition of crab growth.

Tagging data of this nature have been collected (R. Warner, California Department of Fish and Game, 619 2nd St., Eureka, CA 95501, personal communication). Young crabs ranging from 80 to 150 mm were tagged in the summers of 1973 and 1974 and later recovered by fishermen. A plot connecting release size and time to recapture size and time in Fig. 2 generally follows the progression of size modes with a slope of approximately 30 mm/yr. Unfortunately these data do not allow unequivocal separation of the 1972 and 1973 year-classes because of the difficulty in assigning a year-class to the young crabs at the time of tagging.

An illuminating means of summarizing the two types of available data (i.e. size modes in early life and increment per molt in later life) is to plot known size distributions of known ages for the early years of life and project their entry into the fishery assuming a single molt each year at a specified increment (Fig. 7). This representation allows one to project the age at which a crab of a certain size would enter the fishery. Based on the studies referenced herein I have used a growth increment of 28 mm/molt for carapace widths approaching legal size. I have used only those size distributions in early life that can be clearly followed from year to year. Although this plot requires some care in interpretation (e.g. the California Department of Fish and Game 1972 data may actually be two year-classes as noted earlier) it implies that few crabs enter the fishery at ages 3 and 6 and most enter at ages 4 and 5 (ages from hatch).

The results obtained here have significant implications for the interpretation of research on the cause of cycles in the northern California Dungeness crab fishery. With slower growth rate the expected period of cycles produced by any specific mechanism is greater than previously thought. This results from the use of a description of growth in which an age-class enters the fishery at 3.5 and 4.5 yr from metamorphosis rather than being completely recruited at age 3.5 as in previous models (Botsford and Wickham 1978; McKelvey et al. 1980).

The values of expected period computed here depend critically on the weighting function describing the relative effect of older animals at different ages or density-dependent recruitment. We have here assumed for cannibalism that the effect would be roughly proportional to metabolic requirements (weight to the 0.8 power). Greater cannibalism at lower ages would shorten the period and lesser cannibalism at young ages would lengthen the period. This function will be better defined from data taken in ongoing studies of cannibalism. In this regard, recent studies in grays Harbor indicate a high degree of cannibalism by juveniles on newly metamorphosed crabs (Stevens et al. 1982). If cannibalism were by juveniles it would cause a more stable population and cycles of shorter period if there were any.

The stability results with growth patterns used here imply little change in stability point K' (i.e. the rate of change of density-dependent mortality with effective population size that is required to cause cyclic behavior). Unfortunately, the data required to test the rate of change of recruitment mortality with population size are estimates of mortality over a range of population levels and hence require considerable time to collect.

A further change in expected results appears in the actual cycles produced. As the normalized slope of the recruitment survival function (K) is made more negative, these population models typically are initially stable with cycles of decreasing magnitude and then become unstable with cycles that increase in magnitude up to a certain "limit cycle" of constant magnitude. This magnitude is decreased as size structure is added (i.e. the ratio of the amplitude of the cycles to the equilibrium level is less). The reason for this is the prevention of rapid changes by the spread of age-classes over several years. This change in behavior makes the behavior of these models less similar to the observed behavior in the real population (catch in the fishery varies by a factor greater than 20).

With regard to the density-dependent mechanisms under investigation as potential causes of the cycles, neither can be rejected at this time. In terms of the stability condition on the rate of change of recruitment mortality with population size, we do not yet have sufficient data to perform this test. In terms of the period of the cycles, results obtained here indicate a period of approximately 8 yr for cannibalism. For the egg predator, because the point of influence is at the egg stage and the adult weighting function is the fecundity of the unfished female populations, the expected period is greater. Thus, the expected period of cycles based on current model assumptions is lower than the observed period by 1 or 2 yr for cannibalism and approximately the same as the observed period for the egg predator. However, rejection of the cannibalism hypothesis is not appropriate at this time. Better knowledge of the relative age of cannibalism, the actual nature of the density-dependent function, and the influence of environmental variables on the period of the cycles could easily change the period by 2 yr.

There is not complete agreement on the last conclusion. McKelvey et al. (1980) developed a similar model and derived the same result as Botsford and Wickham (1978) that the period of cycles produced by a model with cannibalism (and many assumptions) was less than the observed period, yet they chose to reject the cannibalism hypothesis on that basis. Because of the uncertainty in earlier models the earlier rejection of cannibalism as a possible mechanism causing the cycles (McKelvey et al. 1980) is considered here to have been premature. Both of the two model assumptions examined thus far (constant harvest and growth rates) had led to an increase in period. These results also underline a potential pitfall of the procedure of rejecting a hypothesis because it does not produce the actual observed result when put into a model when the remaining structure of the model is not well known (see Botsford 1981 and McKelvey and Hankin 1981 for further views on this issue). The period of cycles resulting from density-dependent recruitment in a fished population subject to environmental influences is a complex issue. Its use as a diagnostic tool in a poorly defined population involves considerable risk of error.

The synthesis presented here of material on Dungeness crab growth rate also has implications for hypotheses involving environmental variables as the cause of these cycles. Since most evaluation of these hypotheses is based on statistical comparison of time series of environmental variables with crab catch or abundance, accurate knowledge of the length of time from the larval phase (the stage at which the environment is most likely to affect crab survival) is necessary to interpret mechanisms. From the results obtained here one would expect a correlation between the catch record and environmental variable at a lag of 4 and 5 yr if it were directly influencing larval survival. If it were affecting growth rate, it could increase the number of individuals entering the fishery at age 3 yr. While density-dependent mechanisms have been the focus of the material presented here, environmental factors are still a potential cause of the cycles and are under active investigation. The facts that (1) the abundance record is more erratic than previously thought (Methot and Botsford 1982), (2) there are covarying cycles of the same period in the northern California chinook salmon (*Oncorhynchus tshawytscha*) fishery (Botsford et al. 1983), and (3) substantial age-classes develop in this fishery even when there is high adult abundance (as indicated by the catch record) as in 1966 lead to serious consideration of environmental factors. These may act in conjunction with one of the density-dependent mechanisms discussed here.

Acknowledgments

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Appendix A

Equation 1 can be rewritten

$$\text{(A1)}\quad \left[\frac{\partial}{\partial a} + g(m, a)\frac{\partial}{\partial m}\right] n(m, a) = -\left[\frac{\partial g(m, a)}{\partial m} + D(m, a)\right] n(m, a).$$

From the chain rule:

$$\text{(A2)}\quad \frac{dn}{da} = \frac{\partial n}{\partial m}\frac{dm}{da} + \frac{\partial n}{\partial a}.$$

Hence, if

$$\text{(A3)}\quad \frac{dm}{da} = g(m, a)$$

the partial differential equation can be written as an ordinary differential equation:

$$\text{(A4)}\quad \frac{d\tilde{n}}{da} = -\,[g_m(m, a) + D(m, a)]\tilde{n}(a)$$

where $\tilde{n}(a)$ is the number at age a. Since the size variable m in g_m and D is $m(a)$ from the solution to equation A3, g_m and D depend only on a.

By separation of variables:

$$\text{(A5)}\quad \ln\left[\frac{\tilde{n}(a)}{\tilde{n}(0)}\right] = -\int_0^a g_m(m, s)ds - \int_0^a D(m, s)ds.$$

From a change of variable:

$$\text{(A6)}\quad \int_0^a g_m(m, s)ds = \int_{m_0}^{m(a)} \frac{g_m(m' a)}{g(m')}\,dm' = \ln\left[\frac{g(m, a)}{g(m_0)}\right]$$

where $g(m) = g(m, a)$. Similarly,

$$\int_0^a D(m, s)ds = \int_{m_0}^{m(a)} \frac{D(m', a)}{g(m')}\,dm'.$$

Hence

$$n(m, a) = n(m, 0)\frac{g(m_0)}{g(m)}\exp\left[-\int_{m_0}^{m} \frac{D(m', a)}{g(m')}\,dm'\right].$$

This equation provides a solution for $n(m, a)$ without the effects of fishing. From this solution we observe that a constant fishing mortality rate for size m_1 and greater will introduce a term of the form

$$F(m) = \exp\left[-E\int_{m_1}^{m} \frac{dm'}{g(m')}\right]$$

as presented in equation 8.

Homing of Atlantic Herring (*Clupea harengus harengus*) in Newfoundland Waters as Indicated by Tagging Data

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Wheeler, J. P., and G. H. Winters. 1984. Homing of Atlantic herring (*Clupea harengus harengus*) in Newfoundland waters as indicated by tagging data. Can. J. Fish. Aquat. Sci. 41:108–117.

An extensive tagging program was carried out on the herring populations along the east coast of Newfoundland during the 1970s as a basis for defining stock management units. The resulting tag recapture data have been examined in relation to the hypothesis that the majority of Atlantic herring (*Clupea harengus harengus*) return to the same area to spawn in successive years. Our analyses support this hypothesis and indicate that homing rates for Atlantic herring are high (approximately 90%). We concluded that herring fisheries restricted to spawning fish would allow a more rational distribution of fishing effort such that individual spawning stocks could be exploited in varying fashion according to the desired management objectives.

Un important programme d'étiquetage des populations de hareng a été réalisé le long de la côte est de Terre-Neuve au cours des années 1970 pour servir de base à la définition des unités de gestion des stocks. Les données fournies par les étiquettes récupérées ont été étudiées par rapport à l'hypothèse selon laquelle la plus grande partie des harengs de l'Atlantique (*Clupea harengus harengus*) retournent au même endroit année après année pour frayer. Nos analyses appuient cette hypothèse et révèlent que, dans le cas de cette espèce, les taux de retour sont élevés (environ 90%). Selon nous, la restriction de la pêche du hareng aux individus reproducteurs permettrait une répartition plus rationnelle de l'effort de pêche ; ainsi, les stocks reproducteurs individuels pourraient être exploités de différentes manières selon les buts gestionnels visés.

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The commercial fisheries that developed on stocks of Atlantic herring (*Clupea harengus harengus*) along the east coast of Newfoundland (Fig. 1) in the early 1970s were conducted throughout most months of the year and by a variety of gears, including a highly mobile purse-seine fleet. An extensive tagging program involving approximately 100 000 tags was carried out on these populations of herring in the 1970s to determine stock relationships and migratory patterns. A preliminary analysis of tag returns from these experiments (Pinhorn 1976) concluded that, for management purposes, the herring can be considered as four stock complexes that exhibit well-defined north–south migratory patterns moving northwards for feeding in summer and southwards back into the bays to overwinter and spawn. The purse-seine fleet tended to exploit migrating concentrations of herring and, therefore, both immature and mature fish from a mixture of stocks. During the early 1980s, however, fishing patterns changed as a result of stock decline; fixed gear fisheries catching mainly spawning fish became the principal source of fishery removals. Harden Jones (1968) concluded that a general homing tendency existed in Atlantic herring in the North Sea; however, the situation is still not clear and scientific opinion is not unanimous (Blaxter and Hunter 1982). If such a homing tendency exists, then herring fisheries exploiting spawning fish may require a much different definition of "unit" stock than fisheries conducted on migrating fish at other times of the year (Hourston 1982). We have therefore analyzed the existent tagging data for east coast Newfoundland herring to determine the extent to which homing occurs and the implications of such homing on stock definition.

A fish spawning in the same season as that in which it was born and returning to spawn on the parent ground may be said to have homed. It is impossible from the Newfoundland tagging studies to show that a fish returns to the parent ground; this would require marking and following the development of larval fish. In this study, homing is defined as returning to the same area to spawn in successive years.

Materials and Methods

Thirty-one tagging experiments were conducted along the east coast of Newfoundland from 1975 to 1981. In addition, six tagging experiments were conducted in St. Mary's Bay during the 1970s (Moores and Winters 1977).

The tagging experiments were designed to include as many areas of the east coast and as many months of the year as was possible. Herring used in the tagging experiments were obtained mainly from commercial gears such as purse seines, bar seines, or traps and were held in special holding pounds (Winters and Beckett 1978) during the tagging operations.

Six types of external tags were used in the experiments (Fig. 2): anchor (Floy FD-68), short anchor (Floy FD-68D), dart (Floy DT-2), streamer (Floy FTSL-73), disc and dangler, and disc and disc. Most (80%) of the tags applied were of the anchor type and each tag was individually numbered and bore the return

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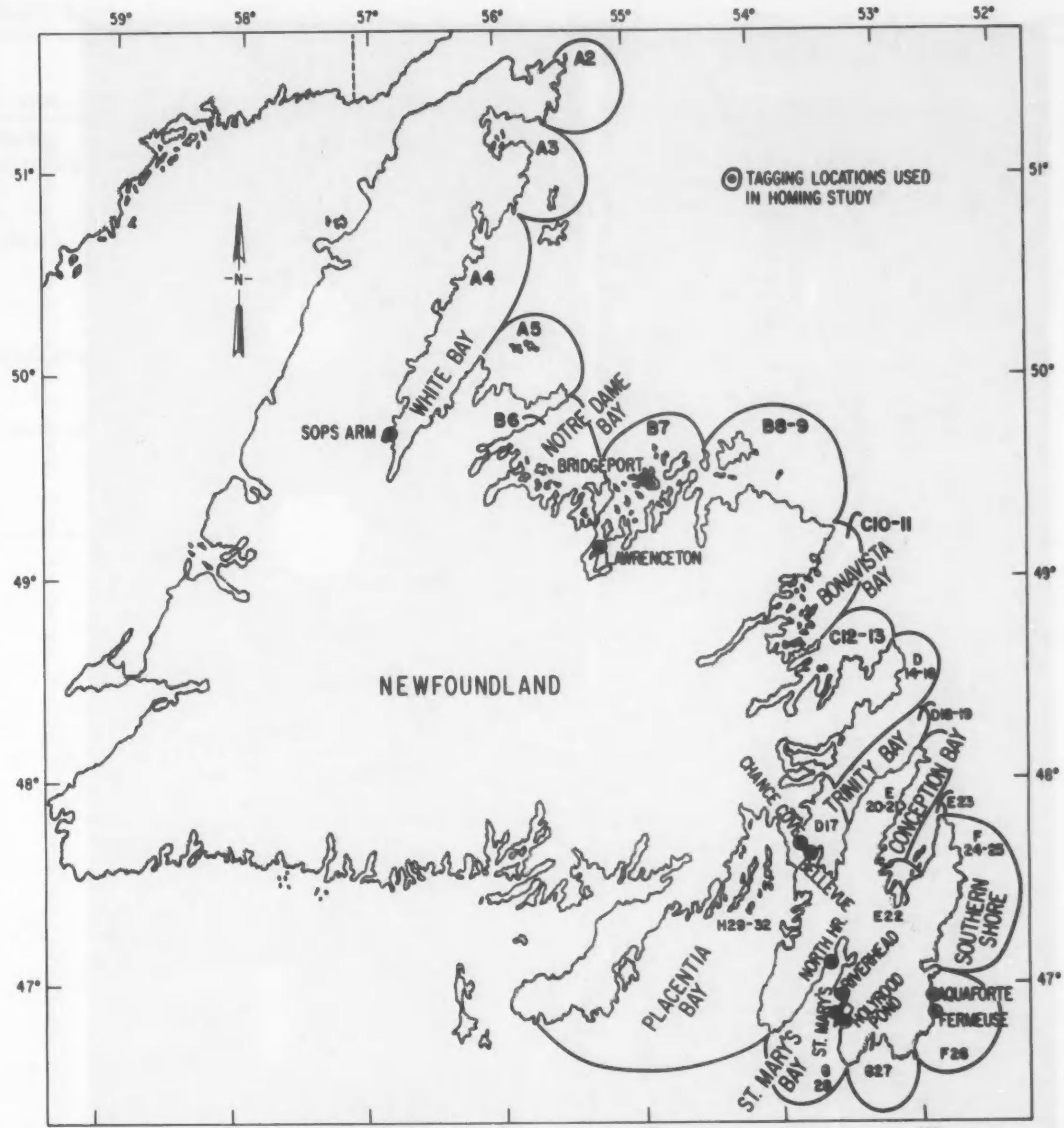
[1] Authors in alphabetical order.


59°
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52°
51°
50°
49°
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A2
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A4
A5
B6
B7
B8-9
C10-11
C12-13
D 14-16
D18-19
D17
E 20-21
E22
E23
F 24-25
F26
G27
G 28
H29-32
TAGGING LOCATIONS USED IN HOMING STUDY
N
NEWFOUNDLAND
WHITE BAY
NOTRE DAME BAY
BONAVISTA BAY
TRINITY BAY
CONCEPTION BAY
PLACENTIA BAY
ST. MARY'S BAY
SOUTHERN SHORE
SOPS ARM
BRIDGEPORT
LAWRENCETON
CHANCE COVE
BELLEVUE
NORTH HR.
RIVERHEAD
ST. MARY'S
HOLYROOD POND
AQUAFORTE
FERMEUSE

FIG. 1. Tagging locations, bays, and statistical sections used to study homing of herring.

address of the Fisheries Research Branch. A reward was paid for each tag returned with information on date of capture, location of capture, and gear used.

Herring from each tagging experiment were sampled for length, weight, sex, and maturity stage composition. Spawning type (spring or fall) was assigned on the basis of maturity stage (Anonymous 1962).

Definition of Homing Area

Tagging experiments selected for this homing study (Table 1) were restricted to spawning fish tagged on or near the spawning grounds in five separate management areas (Fig. 1). In the 13 experiments included for analysis, the majority of fish sampled during tagging were in spawning condition or within several weeks of spawning (maturity stages 4–7 (Anonymous 1962)). Spawning fish (maturity stages 6 and 7) dominated the samples from White Bay, Notre Dame Bay, and St. Mary's Bay. Prespawners (maturity stages 4 and 5) were dominant in Trinity Bay and along the Southern Shore. In all areas, May–June represented the period of peak spawning, and therefore, only recaptures during this period were considered in the analysis of

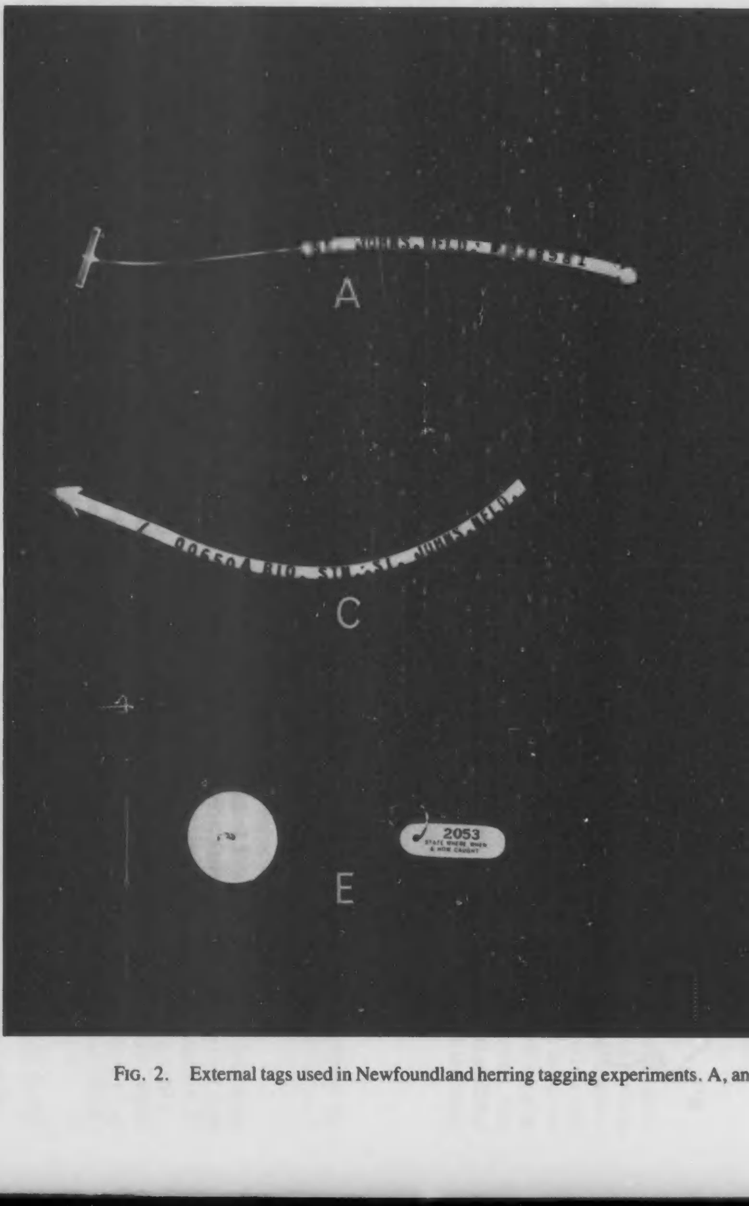
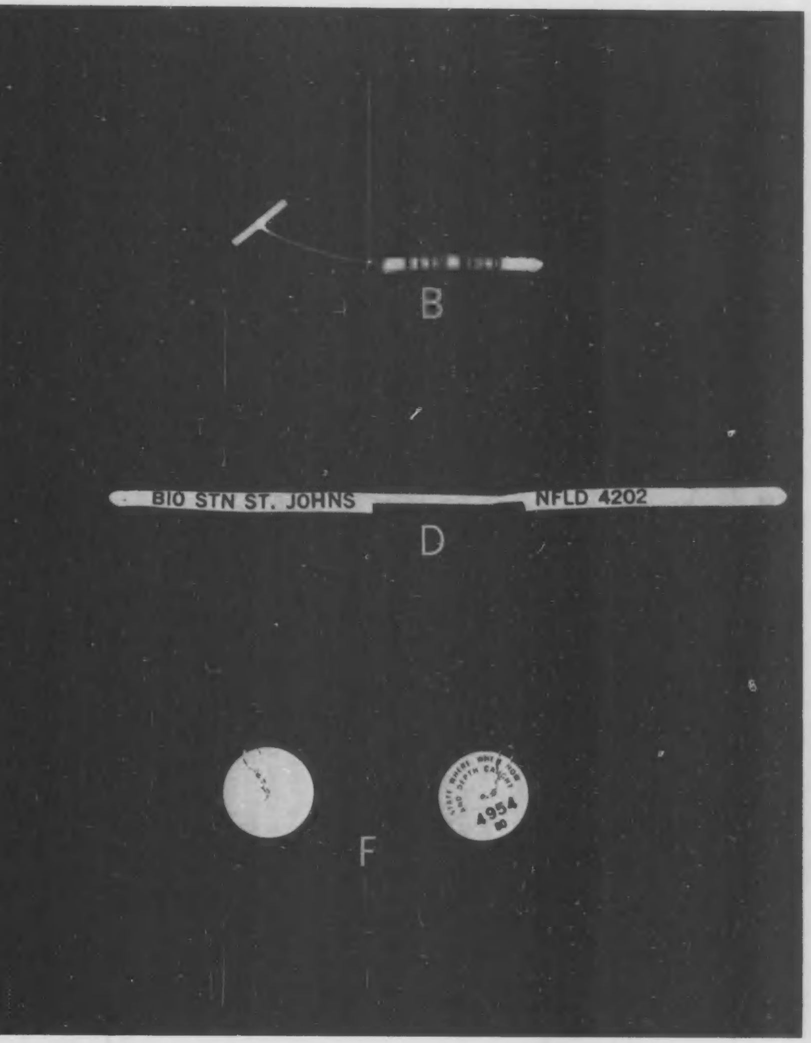

ST. JOHNS, NFLD.
A
00650A BIO. STN. ST. JOHNS, NFLD.
C
2053
STATE WHERE WHEN & HOW CAUGHT
E

FIG. 2. External tags used in Newfoundland herring tagging experiments. A, an


B
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NFLD 4202
D
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4954
80
F

ts. A, anchor; B, short anchor; C, dart; D, streamer; E, disc and dangler; F, disc and disc.

TABLE 1. Location, dates, numbers tagged, and maturity stage information in experiments to study homing of herring in Newfoundland waters.

Area	Locality	Statistical section	Date	No. tagged	No. sampled	Maturity stage (% composition)						
						2	3	4	5	6	7	8
White Bay	Sops Arm	A4	June 1976	5650	100	—	—	—	—	23.0	77.0	—
Notre Dame Bay	Bridgeport	B7	June 1975	950	100	—	—	—	5.0	74.0	21.0	—
	Lawrenceton	B7	May–June 1976	4500	150	—	0.7	—	14.0	18.0	67.3	—
				5400	250	—	0.4	—	10.4	40.4	48.8	—
Trinity Bay	Chance Cove	D17	May 1975	3725	50	—	—	100.0	—	—	—	—
	Chance Cove	D17	April 1976	5000	250	1.6	3.2	94.4	—	—	—	1.3
	Bellevue	D17	May 1977	5000	250	—	2.0	81.6	12.0	0.4	3.6	—
	Bellevue	D17	May 1978	4200	150	—	—	—	18.7	23.3	58.0	—
				17925	700	0.6	1.9	70.1	8.3	5.1	13.7	0.3
Southern Shore	Fermeuse	F26	May 1975	2000	100	—	2.0	50.0	46.0	1.0	1.0	—
	Fermeuse	F26	May 1976	3000	100	8.0	5.0	57.0	28.0	1.0	—	1.0
				5000	200	4.0	32.5	53.5	37.0	1.0	0.5	0.5
St. Mary's Bay	North Harbour	G28	June 1974	6863	200	—	—	—	2.5	7.0	90.5	—
	Holyrood Pond	G28	June 1975	600	100	—	—	—	2.0	8.0	88.0	2.0
	St. Mary's	G28	April 1976	3825	49	6.1	6.1	87.8	—	—	—	—
	Riverhead	G28	May 1977	3000	100	—	—	—	5.0	4.0	91.0	—
				14288	449	0.7	0.7	9.6	2.7	5.8	80.2	0.4

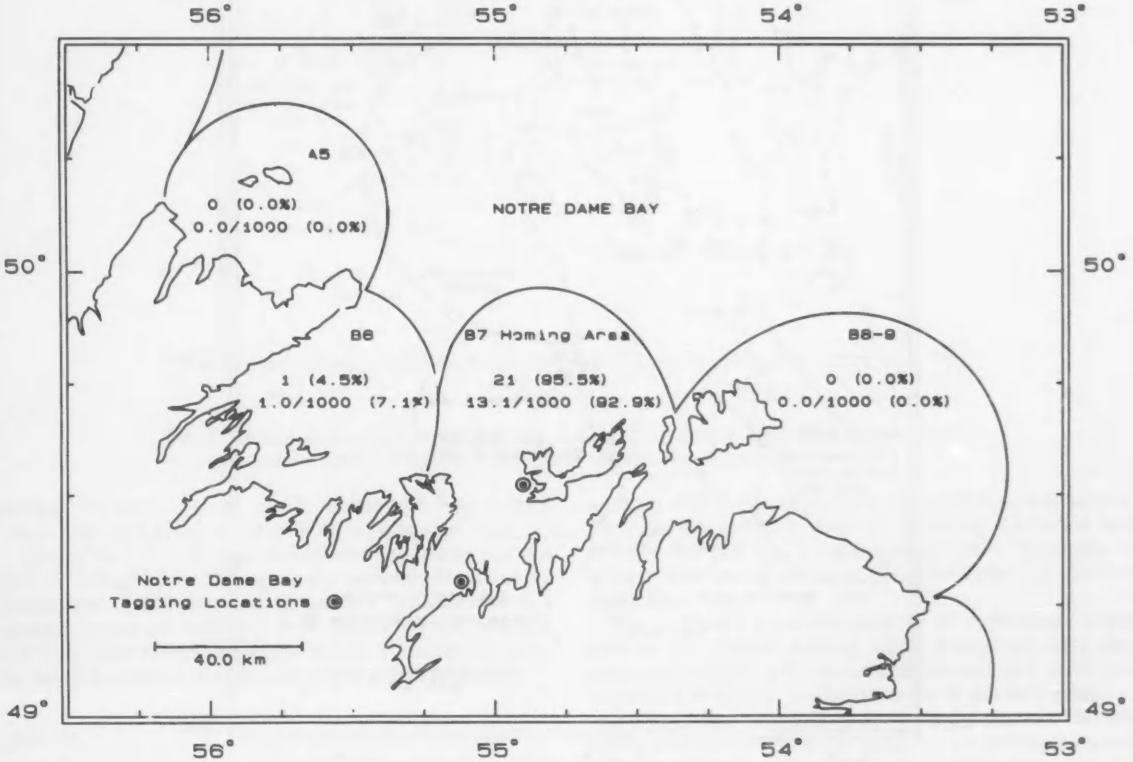
56°
55°
54°
53°
A5
0 (0.0%)
0.0/1000 (0.0%)
NOTRE DAME BAY
50°
50°
B6
1 (4.5%)
1.0/1000 (7.1%)
B7 Homing Area
21 (95.5%)
13.1/1000 (92.9%)
B8-9
0 (0.0%)
0.0/1000 (0.0%)
Notre Dame Bay
Tagging Locations
40.0 km
49°
49°
56°
55°
54°
53°

FIG. 3. Actual tag recaptures (upper number) and adjusted tag recaptures per kiloton of herring landed (lower number) during May–June, by section, for Notre Dame Bay tagging experiments.

TABLE 2. Summary of Newfoundland tagging experiments used to study homing of herring, by area, and homing (statistical) section indicating length of shoreline in homing section, total tag recaptures (excluding recaptures within 1 mo of tagging), recaptures during May and June in years subsequent to tagging, recaptures during these 2 mo from the section where tagging occurred, and homing recaptures adjusted by catch.

Locality	Homing (statistical) section	Shoreline length (km) of homing section	Total No. tagged	Total overall recaptures No.	Total overall recaptures Total tagged	Total May–June recaptures No.	Total May–June recaptures % of total recaptures	Homing recaptures No.	Homing recaptures % May–June recaptures	Adjusted homing recaptures No./kt catch	Adjusted homing recaptures %
White Bay	A4	350	5 650	201	3.6	44	21.9	26	59.1	102.2	92.4
Notre Dame Bay	B7	500	5 450	88	1.6	22	25.0	21	95.5	13.1	92.9
Trinity Bay	D17	180	17 925	367	2.0	75	20.4	62	82.7	124.6	74.7
Southern Shore	F26	100	5 000	110	2.2	30	27.3	10	33.3	59.9	65.5
St. Mary's Bay	G28	250	14 288	253	1.8	104	41.1	95	91.3	157.6	80.7

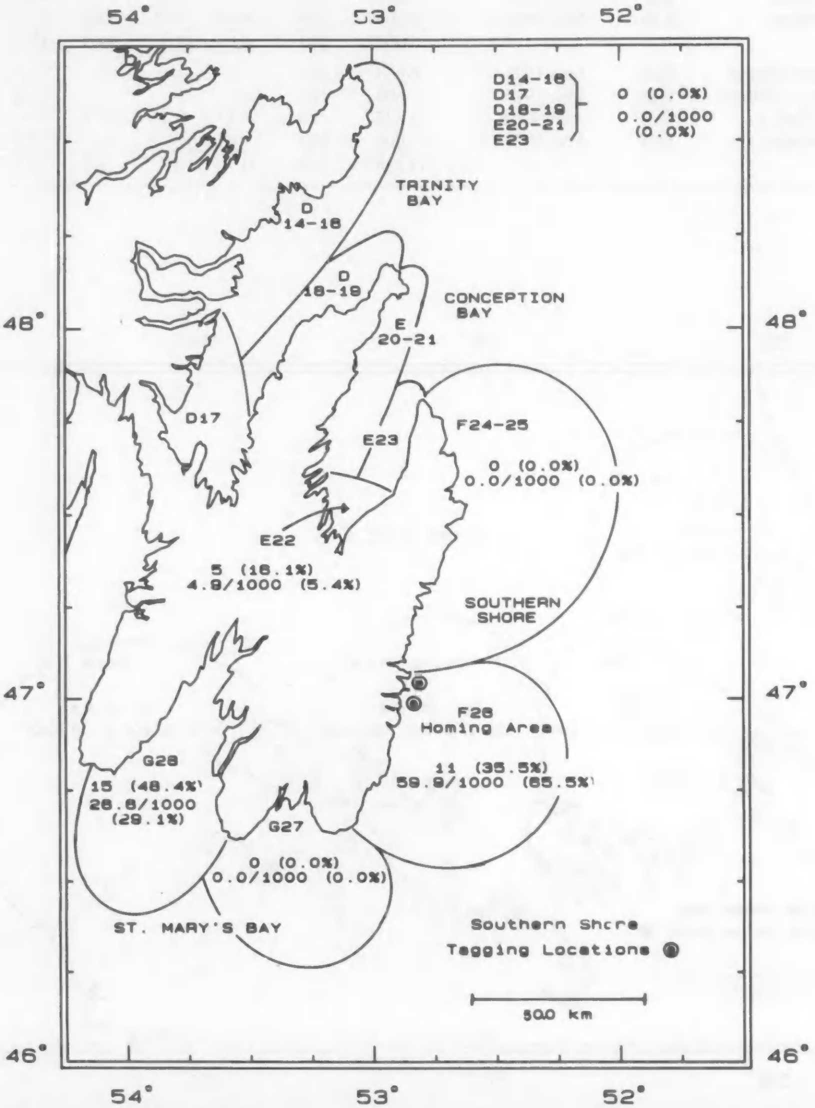
54°
53°
52°
48°
47°
46°
D14-18
D17
D18-19
E20-21
E23
0 (0.0%)
0.0/1000
(0.0%)
TRINITY BAY
D 14-18
D 18-19
CONCEPTION BAY
E 20-21
D17
E23
F24-25
0 (0.0%)
0.0/1000 (0.0%)
E22
5 (16.1%)
4.9/1000 (5.4%)
SOUTHERN SHORE
F26 Homing Area
11 (35.5%)
59.9/1000 (65.5%)
G28
15 (48.4%)
28.8/1000
(29.1%)
G27
0 (0.0%)
0.0/1000 (0.0%)
ST. MARY'S BAY
Southern Shore Tagging Locations
50.0 km

FIG. 4. Actual tag recaptures (upper number) and adjusted tag recaptures per kiloton of herring landed (lower number) during May–June, by section, for Southern Shore tagging experiments.

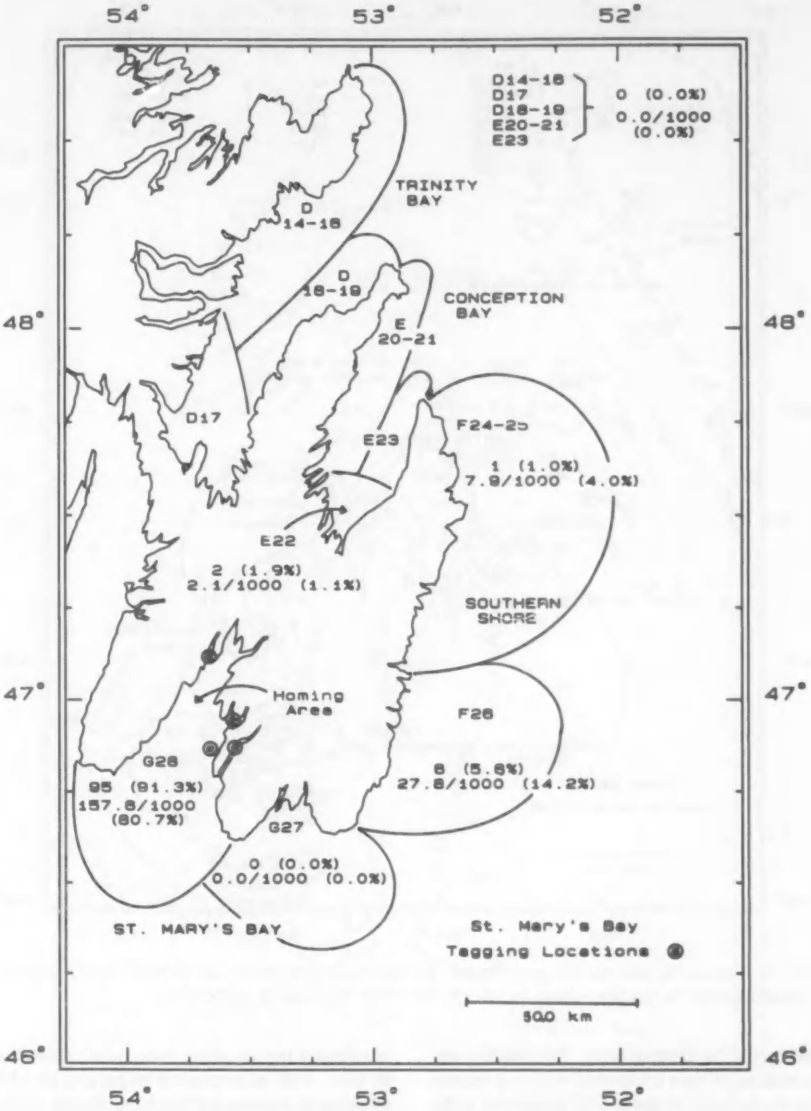
54°
53°
52°
48°
47°
46°
D14-16
D17
D18-19
E20-21
E23
0 (0.0%)
0.0/1000 (0.0%)
TRINITY BAY
D 14-16
D 18-19
CONCEPTION BAY
E 20-21
D17
F24-25
E23
1 (1.0%)
7.9/1000 (4.0%)
E22
2 (1.9%)
2.1/1000 (1.1%)
SOUTHERN SHORE
Homing Area
F26
G26
95 (91.3%)
157.8/1000 (80.7%)
6 (5.8%)
27.8/1000 (14.2%)
G27
0 (0.0%)
0.0/1000 (0.0%)
ST. MARY'S BAY
St. Mary's Bay Tagging Locations ●
50.0 km

FIG. 5. Actual tag recaptures (upper number) and adjusted tag recaptures per kiloton of herring landed (lower number) during May–June, by section, for St. Mary's Bay tagging experiments.

homing intensity, defined as the percent of total returns (May–June period) recovered from the tagging area.

Each of the five study areas was divided into smaller sections (Fig. 1) defined by the Economics and Statistics Branch of the Department of Fisheries and Oceans for calculation of fish landings among communities. These statistical sections vary in size from 100 to 500 km in shoreline length; consequently, some are better than others as indicators of the degree of homing.

Analyses

The date, location of recapture, and gear used were requested with each tag returned. Corrections were made for area, locality, and date of recapture if such information was not included with the tag return or if the information was suspect. These corrections were made by contacting the person who returned the tag and obtaining clarification. Estimates of homing were based on these corrected areas and dates of recapture.

Tag recaptures were combined for all experiments within each of the defined homing areas. Recaptures were then examined within the section where tagging occurred, in all years subsequent to tagging, to determine the degree of homing.

Two methods were used to determine the degree of homing within each of the five study areas: (1) comparing the actual number of tags recovered from the section where tagging occurred with tag returns from adjacent sections and (2) adjusting the number of tag returns by landings within each

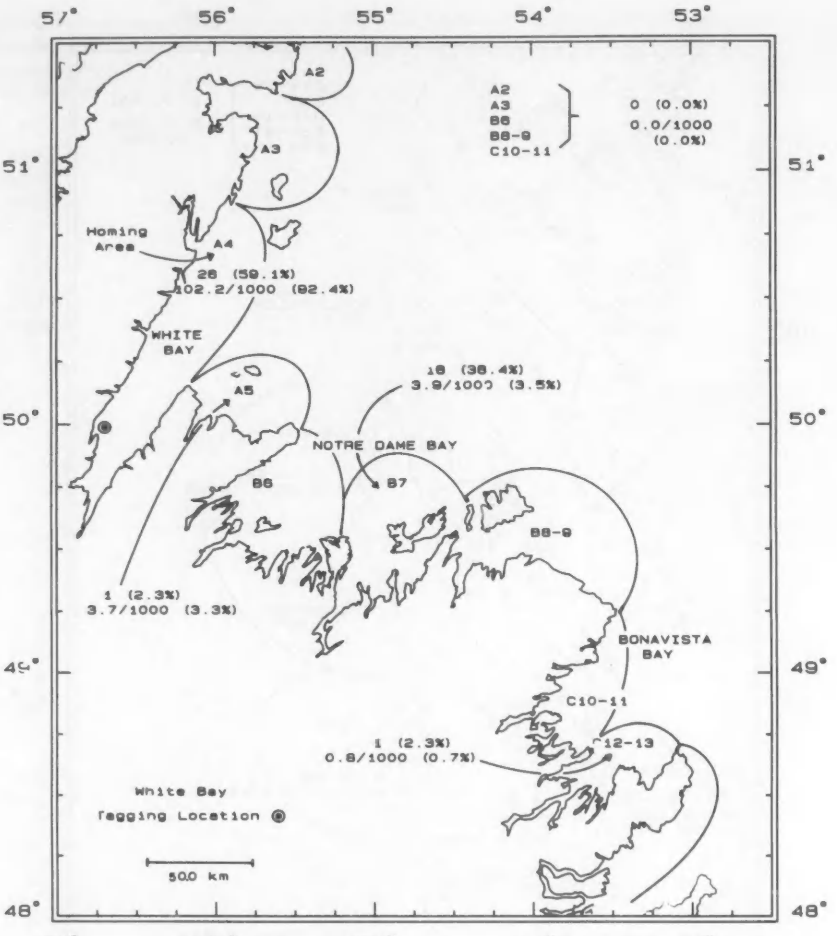

FIG. 6. Actual tag recaptures (upper number) and adjusted tag recaptures per kiloton of herring landed (lower number) during May–June, by section, for White Bay tagging experiment.

section and then making similar comparisons. This adjustment was made, since the number of tags recaptured within a section is dependent not only on the ratio of marked to unmarked in the sampled population but also on the catch and effort within that section. As no measure of comparative effort was available, it was assumed that a unit of catch required the same fishing effort for all areas, and therefore, a correction for catch only was made. This adjustment was made by combining returns of all experiments for May and June each year within each area and then using the combined May–June landings by section and year to determine for each section the number of tags returned per 1000 t landed.

Results

Total recapture rates in the five areas ranged from 1.6 to 3.6% excluding those tags recovered within 1 mo of tagging (Table 2). May–June recaptures represented approximately 25% of total recaptures in four of the five areas; in St. Mary's Bay, 40% of the tags were recovered during this time period. From unadjusted tag recapture data, homing estimates ranged from 35 to 95%, with an average homing rate of 73%. However, when adjusted to account for catch, estimates ranged from 65 to 92%, with an average rate of 81%. In both cases, the Southern Shore represented the poorest homing area and Notre Dame Bay the best. Adjustment of tag returns accounted for an increase in the estimate of homing in two areas and a decrease in the other three.

In Notre Dame Bay, the Southern Shore, and St. Mary's Bay (Fig. 3, 4, and 5), the majority of May–June recaptures came from the tagging site or immediately adjacent sections. However, this was not true for White Bay (Fig. 6) or for Trinity Bay (Fig. 7). When adjusted to account for landings, recapture rates in all areas (Fig. 3–7) declined as distance increased from the tagging site.

For homing to occur, it is necessary that the herring leave the spawning area sometime during the year. Preliminary analyses of tagging data (Pinhorn 1976) have shown that east coast Newfoundland herring migrate northwards out of the bays for summer feeding and return into the bays during the fall to

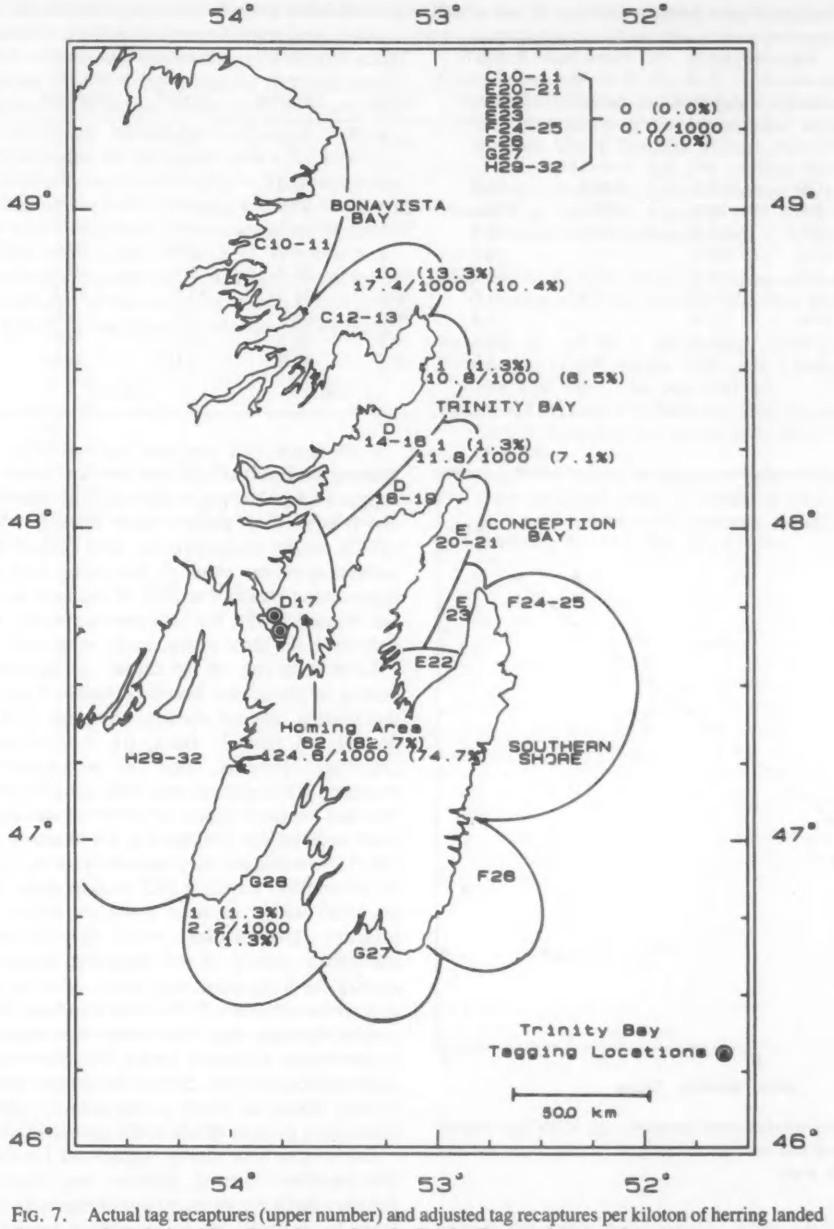
54°
53°
52°
C10-11
E20-21
E22
E23
F24-25
F26
G27
H29-32
0 (0.0%)
0.0/1000
(0.0%)
49°
BONAVISTA BAY
C10-11
10 (13.3%)
17.4/1000 (10.4%)
C12-13
1 (1.3%)
10.8/1000 (8.5%)
TRINITY BAY
D 14-16
1 (1.3%)
11.8/1000 (7.1%)
D 18-19
48°
E 20-21
CONCEPTION BAY
D17
F24-25
E 23
E22
Homing Area
82 (82.7%)
424.6/1000 (74.7%)
H29-32
SOUTHERN SHORE
47°
G28
F26
1 (1.3%)
2.2/1000
(1.3%)
G27
Trinity Bay
Tagging Locations ●
50.0 km
46°

FIG. 7. Actual tag recaptures (upper number) and adjusted tag recaptures per kiloton of herring landed (lower number) during May–June, by section, for Trinity Bay tagging experiments.

overwinter. During this period there is considerable mixing of stocks from adjacent areas. This is further illustrated by the tagging experiments used to study homing (Table 3). In all areas there is a time of the year (generally the fall–winter period) when the majority of recaptures comes from sections other than the section where tagging occurred.

There is a significant correlation between variation in homing intensity between the study areas and the stage of gonad development of the tagged fish. Herring that were tagged while in spawning condition (stages 6 and 7) exhibited much higher rates of homing than those in prespawning condition (Fig. 8; Table 1). We have concluded, therefore, that homing intensity of Newfoundland herring stocks is quite high (about 90%) and is in the same range as homing rates for sockeye salmon (*Oncorhynchus nerka*), which is commonly accepted as the reference species for fish homing (Harden Jones 1968).

Discussion

From tagging studies of Pacific herring (*Clupea harengus pallasi*) on the spawning grounds, Hourston (1982) found an adjusted (excluding certain tag returns) homing rate of 75% or

TABLE 3. Actual and adjusted (per kiloton) percentages of total monthly recaptures taken within the statistical section where tagging occurred.

	White Bay (A4)		Notre Dame Bay (B7)		Trinity Bay (D17)		Southern Shore (F26)		St. Mary's Bay (G28)	
Month	Actual	Adjusted	Actual	Adjusted	Actual	Adjusted	Actual	Adjusted	Actual	Adjusted
January	—	—	—	—	0.0	0.0	0.0	0.0	0.0	0.0
February	—	—	—	—	—	—	0.0	0.0	20.0	93.4
March	0.0	0.0	100.0	100.0	0.0	0.0	—	—	100.0	100.0
April	0.0	0.0	100.0	100.0	21.6	47.9	26.1	171.5	81.1	60.0
May–June	59.1	92.4	95.5	92.9	82.7	74.7	35.5	65.5	91.3	80.7
July	75.0	86.1	0.0	0.0	—	—	0.0	0.0	—	—
August	0.0	0.0	33.3	81.4	61.5	58.4	0.0	0.0	0.0	0.0
September	66.7	27.3	42.9	94.0	70.8	94.5	85.7	77.2	0.0	0.0
October	59.6	22.6	8.3	2.4	26.0	69.4	0.0	0.0	0.0	0.0
November	5.8	66.1	6.7	80.1	8.2	42.4	0.0	0.0	33.3	98.6
December	0.0	0.0	0.0	0.0	14.5	81.9	0.0	0.0	—	—
Total tag returns	73		34		126		23		184	

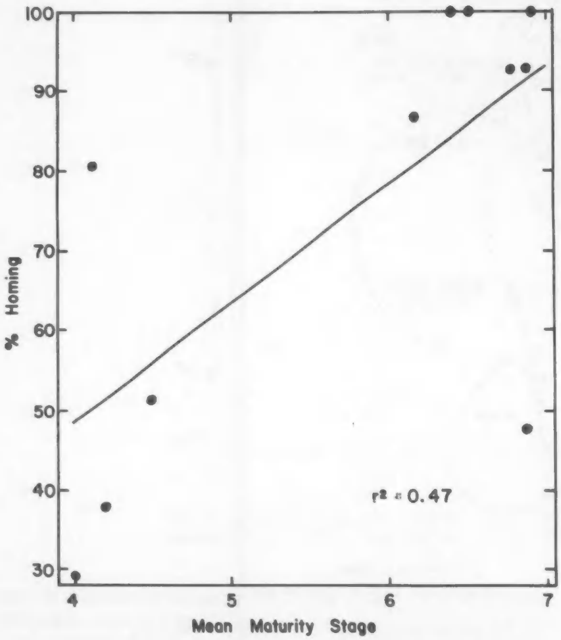

FIG. 8. Relationship between mean maturity stage of herring sampled during May and June and homing intensity of herring from the five Newfoundland study areas.

more in seven of the major fishing areas along the British Columbia coast. Minimum estimates of homing for these seven areas ranged from 27 to 87%, with an average rate of 59%. Similar estimates for the five Newfoundland areas showed an average homing rate of 73%, and this estimate is probably biased downwards due to the inclusion of prespawning fish in the estimates of homing. Further comparisons between the two studies are difficult, as Hourston (1982) did not adjust tag recaptures to account for differences in catch between areas.

Results of this homing study concur with the conclusions of Ware and Henriksen (1978). Based on a study of larval herring growth they concluded that the Gulf of St. Lawrence stock complex consists of discrete spring and autumn spawning groups, each of which has two or more runs. They also suggested that herring return with the same spawning groups and runs as their parents. East coast Newfoundland herring exhibit similar characteristics; they consist of both spring and autumn spawners although the spring component dominates, representing greater than 90% of the catch in all areas (Wheeler and Winters 1982). We have shown that they spawn at the same time, with the same group, in the same area, each year.

Little is known of the causal mechanisms responsible for herring migration and homing. Harden Jones (1968) suggested that herring may not directly recognize a particular spawning ground but innately recognize it as a place suitable for spawning. However, some cue must exist to aid the fish in returning to this general area. Migrating Pacific salmon (*Oncorhynchus nerka*) respond to chemical substances in the home water detectable at a distance by the olfactory organs (Idler et al. 1961). A similar cue may be used by spring spawning herring in Newfoundland waters, which tend to spawn in shallow depths (< 10 m) within or near estuarine waters. However, such olfactory clues, if used, would only be valuable within the immediate vicinity of the spawning grounds and would not explain the long-range migrations exhibited by herring. Tagging studies (Pinhorn 1976) in the Newfoundland area indicate a general denatant migration to overwintering areas, followed by a contranatant migration during the prespawning period. Thus, current direction may serve as the general cue that allows these herring stocks to return to the area of olfactory sensitivity, which then permits return to the parental spawning ground.

Our results have strong implictions for the management of Newfoundland herring fisheries and other Atlantic herring fisheries that have an increasing component of the annual catch taken by fisheries on the spawning grounds. Currently, the Newfoundland east coast is divided into four stock complexes: White Bay–Notre Dame Bay, Bonavista Bay, Trinity Bay, and Conception Bay–Southern Shore (Pinhorn 1976). These management units are based mainly on the interrelationship between seasonal fishing pattern of the purse-seine fleet (mainly on pre- and post-spawning herring) and the seasonal migratory patterns of herring as determined from tagging results. These management units are therefore fairly large and result in the exploitation of mixed spawning stocks, probably in unequal fashion in terms of applied fishing mortality rates. Our results suggest that the spawning group may be a better management unit for any inshore herring fishery, particularly since homing implies that spawning stocks that have been overfished to extinction will only be repopulated by random strayings from adjacent areas. Fisheries restricted to spawning fish on the spawning grounds reduce the possibility of exploiting immature fish and would allow fishing effort on individual spawning stocks to be adjusted according to the prevailing management objective. Further, yield-per-recruit would also be optimized, since the inflexion point of fish growth usually occurs at the time of fish maturation. Since environmental factors rather than egg production appear to account for the major component of recruitment variability in Atlantic herring (Iles and Sinclair 1982; G. H. Winters, E. L. Dalley, and J. A. Moores, unpubl. data), a further advantage of herring fisheries restricted to the spawning season is that catch quotas could be based primarily on economic and/or social factors.

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Influence of Water Level Drawdown on the Fish Populations of Cross Lake, Manitoba

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Gaboury, M. N., and J. W. Patalas. 1984. Influence of water level drawdown on the fish populations of Cross Lake, Manitoba. Can. J. Fish. Aquat. Sci. 41:118–125.

Regulated discharges into Cross Lake, Manitoba, resulted in average summer water volumes in 1980 and 1981 that were 49% lower than preregulated volumes. Water level drawdown in the summer reduces the amount of available habitat. Consequently, the standing crops of lake whitefish (*Coregonus clupeaformis*), walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), and cisco (*Coregonus artedii*) are lower now than in preregulation and early postregulation years. Unusually early and rapid drawdown in March 1981 resulted in a severe winterkill, causing a substantial decrease in catches per unit of effort (CPUE) for most species from 1980 to 1981. The most affected species were whitefish and cisco, which showed a 50% reduction in CPUE from 1980 to 1981. The amount of fall to late spring drawdown and the year-class strengths of coregonid fishes were inversely related. A marked overwinter drawdown reduces whitefish and cisco hatching success apparently by dewatering their spawning areas and desiccating the eggs. Low water levels in spring prevented pike and walleye access to spawning areas.

Au cours des étés 1980 et 1981, les volumes moyens d'eau s'écoulant dans le lac Cross (Manitoba) étaient de 49% moins élevés par rapport à ceux d'avant le réglage du débit. La baisse du plan d'eau en été réduit le nombre d'habitats disponibles. Par conséquent, la biomasse du grand corégone (*Coreganus clupeaformis*), du doré jaune (*Stizostedion vitreum vitreum*), du grand brochet (*Esox lucius*) et du cisco de lac (*Coregonus artedii*) est actuellement moins élevée que pendant les années d'avant la régulation du débit ou au tout début de celle-ci. Une baisse exceptionnellement hâtive et rapide du plan d'eau en mars 1981 a entraîné une forte mortalité hivernale qui s'est traduite par une baisse importante des prises par unité d'effort pour la plupart des espèces par rapport à 1980. Le grand corégone et le cisco de lac, les espèces les plus touchées, ont accusé une baisse de 50% des prises par unité d'effort comparativement à 1980. Il existait une relation inverse entre, d'une part, la baisse du plan d'eau de l'automne à la fin du printemps et, d'autre part, l'abondance des corégonidés d'une classe d'âge. Une baisse prononcée de l'eau pendant la période hivernale diminue le succès de la reproduction du grand corégone et du cisco de lac car les frayères s'assèchent et les oeufs se déshydratent. De faibles niveaux d'eau printaniers ont empêché le grand brochet et le doré jaune d'atteindre les frayères.

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Hydroelectric development of the Nelson River included construction of the Jenpeg generating station to regulate the level of Lake Winnipeg and use it as a storage reservoir for generating stations farther downstream (Dickson 1975). Cross Lake (54°45′N, 97°30′W) (Fig. 1) is immediately downstream of Jenpeg and its water levels have been controlled by tailwater discharges from Jenpeg since 1974. The regulation regime has reversed the pattern of seasonal fluctuations in Cross Lake. Prior to regulation, the mean monthly water levels were highest in the summer, while now they are highest in the winter (Fig. 2).

The eastern portion of Cross Lake was commercially fished from 1959 to 1979, with an average annual harvest of 44 100 kg. Through this period, lake whitefish (*Coregonus clupeaformis*) and walleye (*Stizostedion vitreum vitreum*) were the premium species in the catch, comprising 81 and 17%, respectively. The western portion of the lake, reserved for unlicensed subsistence fishing, has an estimated annual harvest of 40 500 kg of lake whitefish and walleye (Gaboury and Patalas 1982).

Brief fisheries surveys conducted in 1965 (Driver and Doan 1972), 1973 (Ayles et al. 1974), and 1977 (B. H. Wright, Manitoba Department of Natural Resources, unpublished data) provided information on species composition and catch per unit of effort (CPUE). Koshinsky (1973) predicted that under the proposed hydroelectric operating regime at Jenpeg, productivity of lake whitefish, walleye, and northern pike (*Esox lucius*) would be reduced in Cross Lake because of lower summer levels and increased water level fluctuations.

Reports of catch declines by commercial and unlicensed fishermen in Cross Lake prompted this study to determine the impact of the current water level regime on lake morphometry and fish population dynamics.

Study Area

The west basin of Cross Lake consists of narrow, deep river channels as well as shallow lake areas, while the east basin is uniformly shallow. Since the Nelson River flows only through the west basin, the retention time is much shorter here than in the east basin. As the influence of Nelson River flows decreases from west to east, conductivity and total dissolved solids also decrease, while nutrient and organic carbon concentrations increase (Table 1). Similarly, mean plankton biomass is much

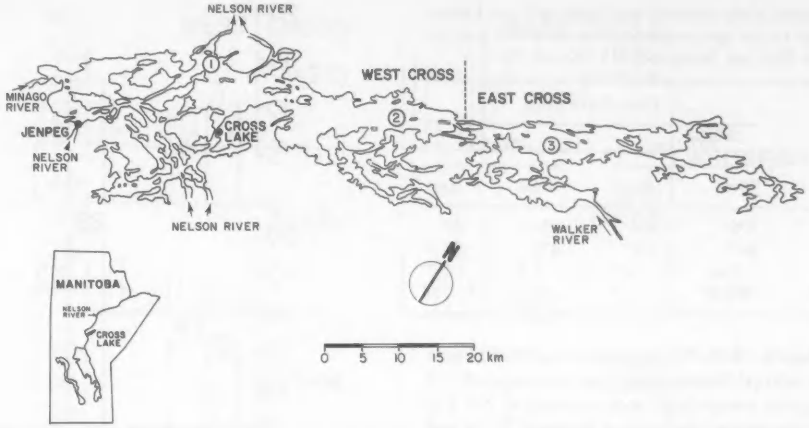

FIG. 1. Cross Lake showing locations of limnological stations (circled numbers).

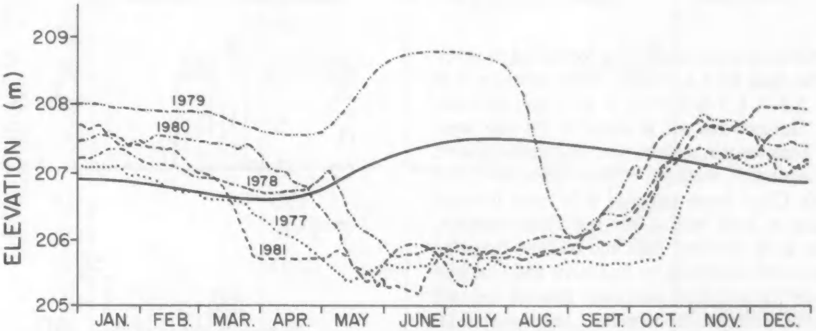

FIG. 2. Comparison of the average monthly water levels on Cross Lake under unregulated conditions (1918–73) (solid curve) and the daily levels recorded under regulation (1977–81) (data provided by the Manitoba Water Resources Branch). Standard error of unregulated hydrograph is ±0.10 m for each month.

TABLE 1. Physicochemical water quality and plankton biomass in Cross Lake, presented as means of monthly measurements from June through September (data from Cleugh 1974; Gaboury and Patalas 1981, 1982).

	1973	1980			1981		
Parameter	Stn. 1	Stn. 1	Stn. 2	Stn. 3	Stn. 1	Stn. 2	Stn. 3
Conductivity ($S \cdot cm^{-1}$)	277	289	220	139	314	196	118
Total dissolved solids ($mg \cdot L^{-1}$)	186	208	155	100	203	137	90
Total suspended solids ($mg \cdot L^{-1}$)	15	11	30	39	20	19	34
Total organic carbon ($mg \cdot L^{-1}$)	8.6	11.8	15.6	20.1	10.8	15.1	18.4
Total phosphorous ($mg \cdot L^{-1}$)	0.04	0.04	0.07	0.08	0.04	0.07	0.06
Total nitrogen ($mg \cdot L^{-1}$)	0.48	0.48	0.68	1.09	0.50	0.83	0.98
Plankton biomass ($mg \cdot m^{-3}$)	—	60	730	979	90	380	518

greater in the east than in the west basin. The water chemistry in the west basin in 1980 and 1981 was similar to that in 1973 (Cleugh 1974); however, there are no previous data on water chemistry in the east basin.

Materials and Methods

Morphometric Measurements

Cross Lake was sounded at a benchmark reference of 205.8 m, the average level recorded between May and September in 1980 and 1981. Aerial photographs were also taken to determine the shoreline at this lake level. The shoreline and depth contours at 205.8 m were transposed onto a map mozaic of Cross Lake composed of photographs taken at a high stage of 207.8 m. Calculations of lake area, volume, and mean depth at stages of 205.8 and 207.8 m were performed according to procedures described by Hutchinson (1957). Lake area at a stage of 207.1 m (historic mean open water stage) (Manitoba

TABLE 2. Morphometry of the west and east basins of Cross Lake at 207.1 m (historic stage for the open water season) and at 205.8 m (the average level between May and September in 1980 and 1981).

	Cross Lake stage			
	207.1 m		205.8 m	
Parameter	West	East	West	East
Area ($10^6 \cdot m^2$)	328	130	254	87
Volume ($10^6 \cdot m^3$)	847	198	470	58
Mean depth (m)	2.6	1.5	1.8	0.7
Maximum depth (m)	23.3	3.2	22.0	1.9

Water Resources Branch 1918–82) was determined from linear interpolation of the radii (r) (where area = πr^2) at stages 207.8 and 205.8 m. Using the interpolated area, volume at 207.1 m was calculated by determining the volume between 207.1 and 205.8 m and adding it to the volume at 205.8 m.

Fisheries

Fish were captured using a standard gang consisting of seven gill nets, each 22.9 m long by 1.8 m deep. Mesh sizes were in the following order: 3.8, 5.1, 7.6, 9.5, 10.8, 12.7, and 13.3 cm, stretched measure. Gangs were set at about 17:00 and were collected 16 h later. Fork length, weight, sex, and maturity were determined for lake whitefish, walleye, northern pike, and cisco (*Coregonus artedii*). Cisco were sampled only from the east basin of Cross Lake in both years. For age determination, opercula were taken from northern pike and otoliths from the other species. Procedures described by Snedecor and Cochran (1967) were followed for statistical analyses. Annual survival rates were computed according to Robson and Chapman (1961). The mean weighted age at onset of sexual maturity was calculated according to Abrasov (1967). Growth of fish was described using the von Bertalanffy model as outlined in Ricker (1975). For a more detailed description of sampling methods see Gaboury and Patalas (1981, 1982).

Results

Environment

Cross Lake water level decreased 1.7 m below the historic mean open water stage of 207.1 m at the minimum discharge from Jenpeg of ~20 $m^3 \cdot s^{-1}$. At 205.8 m, total lake area and volume had declined by 26 and 49%, respectively (Table 2). The west basin with its deep river channels and steep shorelines was less affected by drawdown than the east basin, where area and volume decreased by 33 and 71%, respectively, at 205.8 m. Most of the rock and cobble substrates in the lake were exposed under drawdown.

Bottom water temperatures in both basins were between 20 and 22°C for extended periods during July and August in 1980 and 1981. Maximum surface water temperatures of 26°C were recorded. Summer dissolved oxygen levels at the bottom ranged between 7.0 and 14.7 $mg \cdot L^{-1}$. Winter levels at the surface were between 7.1 and 12.9 $mg \cdot L^{-1}$ near the influence of river flows and between 0.9 and 2.4 $mg \cdot L^{-1}$ in areas where large tracts of submerged vegetation occurred in the summer.

Fisheries

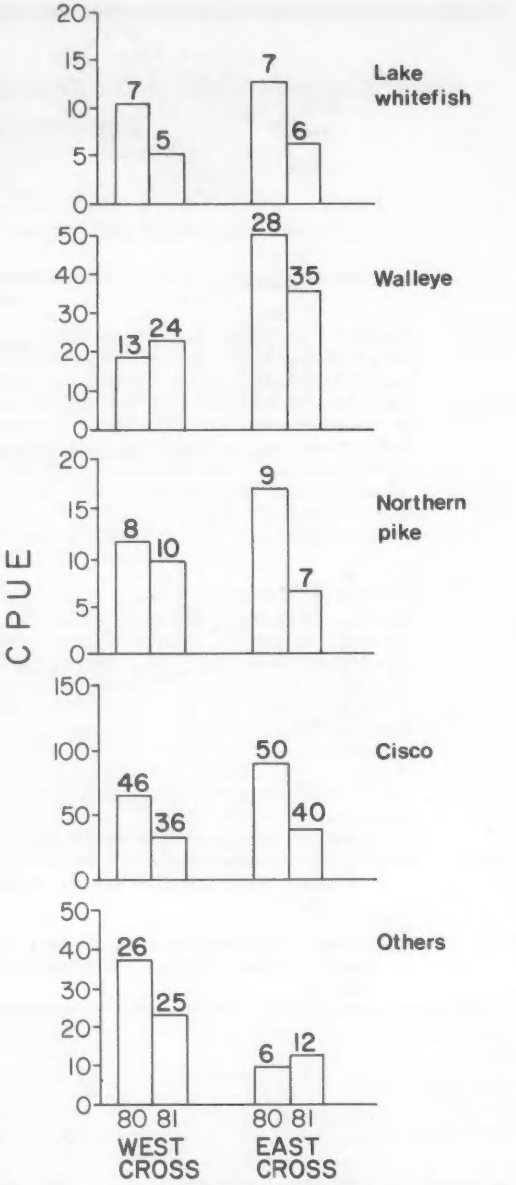

FIG. 3. Comparison of CPUE (number·standard gang^{-1}·16 h^{-1}) and relative abundance (in % above bars) for fish captured in Cross Lake in 1980 and 1981 (see text for other species).

Cisco was the most abundant species in catches in 1980 and 1981, averaging 43% of the total catch, followed by walleye (24%), northern pike (9%), and lake whitefish (6%) (Fig. 3). Other species caught, in order of abundance, included white sucker (*Catostomus commersoni*), yellow perch (*Perca flavescens*), mooneye (*Hiodon tergisus*), sauger (*Stizostedion canadense*), shorthead redhorse (*Moxostoma macrolepidotum*), longnose sucker (*Catostomus catostomus*), freshwater drum (*Aplodinotus grunniens*), goldeye (*Hiodon alosoides*), burbot (*Lota lota*), and common carp (*Cyprinus carpio*). From 1980 to 1981, walleye increased in relative abundance, cisco decreased,

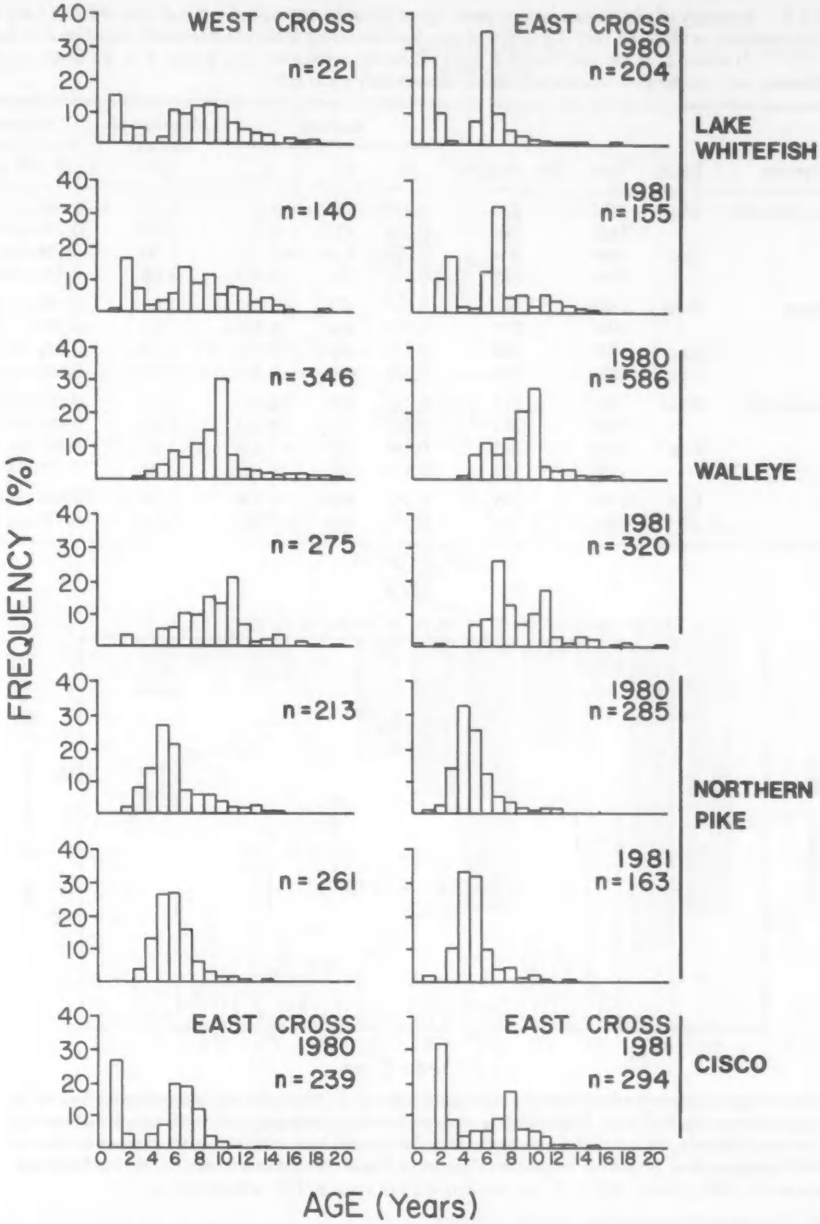

FIG. 4. Age–frequency distributions of lake whitefish, walleye, northern pike, and cisco caught in Cross Lake in 1980 and 1981.

and lake whitefish and northern pike remained unchanged. CPUE of lake whitefish, northern pike, and cisco decreased in both basins of Cross Lake from 1980 to 1981. CPUE of walleye increased in west Cross but decreased in east Cross. Lake whitefish and cisco showed the greatest declines, with CPUE 50% lower in 1981 than in 1980. Fish survival rates between 1980 and 1981 and between basins did not change significantly (Table 3).

Covariance analysis of Brody regressions indicated that the growth rates of lake whitefish, walleye, and northern pike were different ($P < 0.05$) between the east and west basins (Gaboury and Patalas 1981, 1982). For each species, the mean age at onset of sexual maturity (sexes combined) was similar between basins and between years (Table 3).

Fewer older lake whitefish and northern pike were caught in the east basin than in the west basin of Cross Lake (Fig. 4). Walleye had similar age distributions in both basins. Lake whitefish and cisco had bimodal age distributions with relatively

TABLE 3. Summary of growth parameters, mean age of maturity, and annual survival rates of Cross Lake fish (sexes combined) in 1980 and 1981. Growth was calculated according to the von Bertalanffy equation $L_t = L_\infty(1 - e^{-K(t - t_0)})$ where L_t is the fork length at age t, L_∞ is the asymptotic fork length, K is the Brody growth coefficient, and t_0 is the time when length would theoretically equal zero.

Species	Basin	Year	No. sampled	Growth			Mean age of maturity (yr)	Annual survival rate (S ± 2 SE)
				K	L_∞	t_0		
Lake whitefish	West	1980	221	0.239	530	−0.232	5.50	0.567±0.127
		1981	140	0.256	523	−0.451	5.93	0.731±0.055
	East	1980	204	0.304	529	−0.312	5.30	0.526±0.164
		1981	155	0.305	531	−0.473	6.06	0.720±0.078
Walleye	West	1980	346	0.217	477	−0.265	7.65	0.723±0.105
		1981	275	0.227	464	−0.439	7.63	0.574±0.057
	East	1980	586	0.222	462	−0.838	7.38	0.651±0.166
		1981	320	0.186	466	−1.201	7.48	0.697±0.038
Northern pike	West	1980	213	0.147	945	+0.057	3.95	0.600±0.092
		1981	261	0.211	784	+0.184	4.05	0.490±0.082
	East	1980	285	0.144	897	−1.128	3.07	0.465±0.108
		1981	163	0.131	947	−0.763	3.49	0.476±0.078
Cisco	East	1980	239	0.392	404	−0.436	2.90	0.444±0.051
		1981	294	0.372	410	−0.793	3.36	0.525±0.100

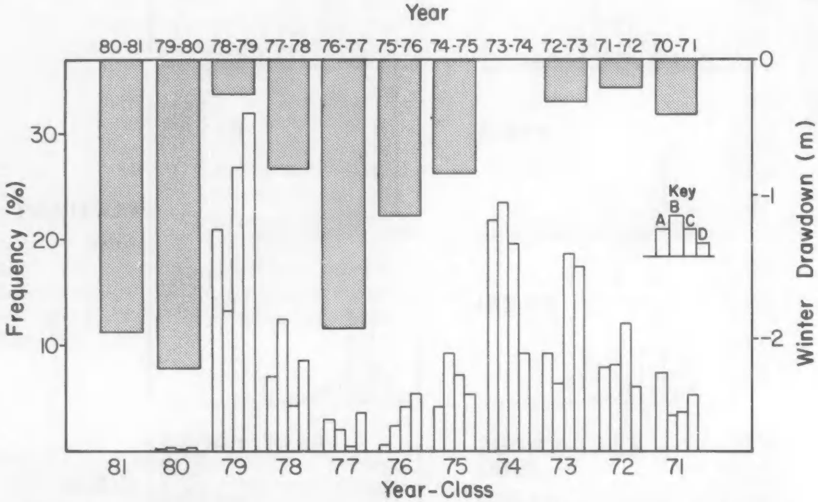

FIG. 5. Relationship between winter to spring drawdown in Cross Lake and lake whitefish and cisco year-class success, 1971–80. Winter and spring drawdown was calculated as the minimum level between October 28 and May 31 subtracted from the level on October 28. A, percent frequency of lake whitefish in 1980 gillnet catches; B, percent frequency of lake whitefish in 1981 gillnet catches; C, percent frequency of cisco in 1980 gillnet catches; D, percent frequency of cisco in 1981 gillnet catches.

strong 1974 and 1979 year-classes and weak 1975–78 year-classes.

An inverse relationship was found between the strengths of lake whitefish and cisco year-classes produced in 1971–80 and the difference between water levels at spawning time (October 28) and the lowest water level until the end of May (Fig. 5). Weak year-classes of lake whitefish and cisco were produced in years with a marked winter or spring drawdown, and strong year-classes appeared in years with little drawdown.

Observations on Fish Movements and Winterkill

In May 1981, walleye were observed congregating below known spawning tributaries made inaccessible by low water levels, and known spawning areas for northern pike were dewatered prior to spawning. In late October 1981, lake whitefish were found congregating at a known spawning area in the west basin of Cross Lake. It was apparent that the lake whitefish were spawning on submerged rocky reefs in river channels.

In March 1981, fish kills occurred in shallow bays and channels that were dewatered as a result of drawdown. The affected species were white sucker, walleye, and lake whitefish. Other species may have been killed but the ice cover prevented an accurate determination of the extent of the fish kill.

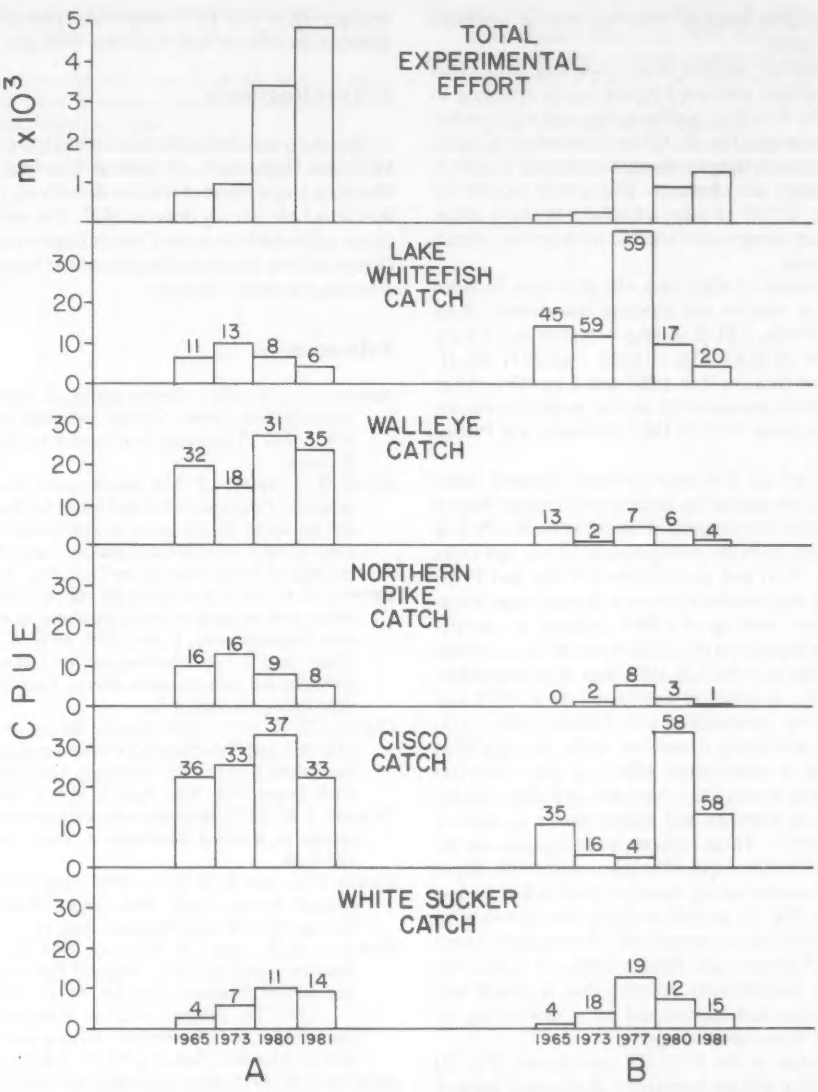

FIG. 6. Comparison of total effort, CPUE (number·100 m^{-1}·d^{-1}), and relative abundance (in % above bars) for fish captured in Cross Lake (both basins combined). (A) CPUE in 7.6-, 9.5-, 10.8-, and 13.3-cm meshes, common to the 1965 (Driver and Doan 1972), 1973 (Ayles et al. 1974), 1980, and 1981 surveys; (B) CPUE in 13.3-cm mesh, the only mesh used in the 1977 survey (B. H. Wright, unpublished data).

Discussion

Differences in physicochemical water quality, plankton biomass, and fish catches indicated that the east basin was more productive than the west basin. The two basins also supported discrete fish populations, as shown by the differences in growth rates and age distributions. Annual harvests of lake whitefish and walleye averaged 3.4 and 1.2 kg·ha^{-1} in the east and west basins, respectively. These yields suggest a higher level of exploitation in east Cross Lake contributing to fewer older fish and significantly faster growth rates in comparison with west Cross Lake.

Unusually early and rapid drawdown in March 1981 (Fig. 2) and low oxygen levels caused a winterkill, which contributed to the dramatic decrease in CPUE of Cross Lake fish from 1980 to 1981. Nonsignificant changes in fish survival rates from 1980 to 1981 suggested that all age-classes were affected by the winterkill. Decreases in CPUE were greater in the east than in the west basin. This was due to the winterkill being more severe in the east basin because of the lack of deepwater habitat for overwintering fish (maximum depth 1.9 m). Also, the west basin had generally higher winter dissolved oxygen concentrations due to the influence of the Nelson River. Evidence of stress was also found in the subsistence fishing census records, which indicated a three- to five-fold increase in CPUE of all species during late March 1981 (Gaboury and Patalas 1982). Increased fish movement probably resulted from the loss of available habitat and anoxic stress.

The 1st yr of extreme summer drawdown was 1977. This reduction in lake volume increased fish densities, resulting in higher CPUE for lake whitefish, northern pike, and white sucker than in preregulation years (Fig. 6). Cisco did not show a higher CPUE, perhaps because netting locations were biased to capture lake whitefish in deepwater channels. This would account for the extremely high CPUE of lake whitefish. Walleye abundances were not truly represented because of their low vulnerability to 13.3-cm nets.

Postregulation catches of adult lake whitefish have declined substantially, both in relative and absolute abundance. Under similar low water levels, CPUE of lake whitefish in 13.3-cm mesh declined from 38 fish$\cdot$100 m$^{-1}\cdot$night^{-1} in 1977 (B. H. Wright, unpublished data) to 9 in 1980 and 4 in 1981. Also, CPUE of lake whitefish decreased by similar proportions in the east and west basins from 1977 to 1981 (Gaboury and Patalas 1982).

Standing stocks of all fish species have declined since regulation, probably because of the reduction of summer habitat under the current water level regime. Comparisons of CPUE in mesh sizes common to both the preregulation (Driver and Doan 1972; Ayles et al. 1974) and postregulation (1980 and 1981) surveys suggest that fish densities have not changed significantly (Fig. 6). However, with up to a 49% decrease in summer water volume under drawdown the standing stocks of fish would be considerably lower in 1980 and 1981 than in preregulation years. Unfortunately, insufficient fishing efforts in 1965 and 1973 prevent confident comparisons with 1980 and 1981 data.

Increased winter and spring drawdown under the regulation of Cross Lake had a pronounced effect on the year-class strengths of coregonid fishes. Lake whitefish and cisco usually spawn in late fall on boulders and coarse stones in shallow depths (Machniak 1975). These substrates are common on the shores of Cross Lake but are exposed at low water levels. Rapid decreases in water levels in spring have occurred in 4 of the last 5 yr since regulation (Fig. 2), and fall to spring drawdowns of up to 2.2 m have occurred, as compared with the average natural variation of 0.8 m (Gaboury and Patalas 1982). It is believed that drawdown has detrimentally affected lake whitefish and cisco hatching success and recruitment by a dewatering of spawning areas and desiccation of eggs.

The low frequencies of the 1975–78 year-classes (Fig. 5) cannot be explained by gill net selectivity. A standard gang of gill nets tends to underestimate the relative frequencies of smaller fish, but as fish size increases, efficiency of capturing a greater proportion of the fish in successively larger size groups increases (Hamley 1975). Accordingly, the 1975–78 year-classes should be better represented than the 1979 year-class.

Although the effect of drawdown on coregonid year-class strengths, to our knowledge, has not been previously documented for lakes below generating stations, this inverse relationship has been found for lake whitefish inhabiting reservoirs (Ioganzen and Podlesnyi 1958; Smirnov 1964 (cited in Machniak 1975)) and for spring spawners when drawdown occurs just prior to spawning (Jester 1971; Benson 1973). June (1970) found that large numbers of atretic eggs in the ovaries of northern pike were associated with drawdown prior to spawning. Spawning of Cross Lake walleye and northern pike was also detrimentally affected by drawdown. Poor representation in the experimental net catches of walleye and northern pike younger than the 1976 year-class precluded a comparison between drawdown and year-class strengths.

Acknowledgments

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Relationship between Otolith Microstructure and the Growth of Juvenile Chum Salmon (*Oncorhynchus keta*) under Different Prey Rations[1]

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Volk, E. C., R. C. Wissmar, C. A. Simenstad, and D. M. Eggers. 1984. Relationship between otolith microstructure and the growth of juvenile chum salmon (*Oncorhynchus keta*) under different prey rations. Can. J. Fish. Aquat. Sci. 41: 126–133.

Effects of different prey taxa and daily ration levels on fish growth and the relationship between fish growth rate and mean otolith increment width were investigated for juvenile chum salmon (*Oncorhynchus keta*) in saltwater aquaria. Growth was positively correlated with ration, and food conversion efficiency was much higher for fish fed the harpacticoid copepod, *Tigriopus californicus*, than either the calanoid copepod, *Pseudocalanus minutus*, or the gammarid amphipod, *Paramoera mohri*. Otolith increments were produced daily for at least the first 160d after hatching and there was a direct relationship between mean daily otolith increment width and fish growth rate. These results illustrate the possibility that otolith microstructure recapitulates juvenile chum growth histories during estuarine residence.

On a étudié les effets de différents taxons de proie et des rations alimentaires quotidiennes sur la croissance des poissons ainsi que la relation entre le rythme de croissance des poissons et la largeur moyenne de l'accroissement des otolithes pour de jeunes saumons kétas (*Oncorynchus keta*) gardés dans des aquariums alimentés en eau salée. On a trouvé une corrélation positive entre la croissance et la ration alimentaire ; en outre, la transformation de la nourriture était beaucoup plus efficace pour les poissons nourris du copépode harpacticoïde, *Tigriopus californicus*, que du copépode calanoïde, *Pseudocalanus minutus*, ou de l'amphipode du groupe des gammaridés, *Paramoera mohri*. Il y a eu accroissement des otolithes chaque jour pour au moins les 160 premiers jours après l'éclosion et il y avait une relation directe entre la largeur moyenne quotidienne de l'accroissement des otolithes et le rythme de croissance des poissons. Ces résultats indiquent la possibilité que la microstructure des otolithes récapitule l'histoire de la croissance des jeunes saumons au cours de leur séjour dans les estuaires.

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Epibenthic harpacticoid copepods represent the predominant prey for 40–70 million juvenile (30–50 mm fork length) chum salmon (*Oncorhynchus keta*) early in their outmigration through estuaries of Puget Sound, with gammarid amphipods second in importance (Simenstad et al. 1982b). Simenstad and Salo (1982) found that large depressions in epibenthic zooplankton abundance during this salmon outmigration through Hood Canal appeared coincident with massive hatchery releases of chum and that the estuarine residence time of these juvenile fish was inversely related to prey abundance. They suggested that insufficient zooplankton prey limit the production of salmon in the estuary.

However, our ability to evaluate estuarine growth and residence time of juvenile salmon has been traditionally hindered by inadequate methods, particularly for the smaller juvenile chum salmon. The commonly used mark and recapture method of estimating juvenile salmon growth rates (Bax and Whitmus 1981) suffers from several drawbacks that can severely reduce the accuracy of growth estimates: (1) possible tagging effects on fish growth, (2) the need to mark huge numbers of fish to obtain significant recaptures, (3) size-related mortality between marking and recapture of a group, and (4) the need for reasonably long periods between marking and recapture.

An alternative method for determining the growth rates of juvenile fish is the use of periodic patterns in their otoliths (or ear stones). (In this paper, otolith refers to the sagittae, the largest pair of calcareous otic elements found in the sacculus of the membranous labyrinth.) Daily increments in fish otoliths have been shown for a variety of marine and freshwater species (Brothers et al. 1976; Taubert and Coble 1977; Marshall and Parker 1982; Neilson and Geen 1982; and others), and otolith development has been demonstrated to be proportional to fish growth (Ralston 1976; Blacker 1974; Marshall and Parker 1982; and others). Growth rates can be calculated using otolith size–fish size and fish size–age relationships (Ralston 1976; Struhsaker and Uchiyama 1978; Wilson and Larkin 1982). The major advantage of this method is its direct application to individual fish, which provides information on variation in a fish's growth, while eliminating the bias imposed by size-selective mortality. Second, this method reduces the number of samples required to estimate growth rates from size-frequency distributions. This paper reports laboratory experiments that examined the relationship between changes in otolith increment width and juvenile chum salmon growth rates under varying regimes of prey ration and taxa.

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Materials and Methods

Aquarium Experiments

The effects of prey ration and taxa on chum growth were investigated in saltwater aquaria. Ten-litre plastic aquaria were connected in series to the University of Washington Friday Harbor Laboratory's (San Juan Island, WA) seawater system and maintained outdoors in the shade. In-line Nitex filters (225 μm) prevented the introduction of extraneous prey organisms and prey from escaping the enclosures. Physical conditions were ambient over the 8-wk experimental period (March–May); temperature averaged 8.9 ± 0.52°C (range 7.6–10.2°C) and salinity averaged 32.7 ± 0.54‰ (range 29.8–33.6‰).

Chum salmon hatched in egg boxes from Beverton Creek, San Juan Island, were transferred directly to full-strength seawater after yolk absorption and fed ad libitum on Oregon Moist Pellets®. For 3 d prior to the initiation of experiments they were fed their respective prey organisms. Prey species used in this study were the calanoid copepod, *Pseudocalanus minutus* (351–500 μm), the epibenthic harpacticoid copepod, *Tigriopus californicus* (351–500 μm), and the gammarid amphipod, *Paramoera mohri* (500–1000 μm). Details of their collection, culture, and characteristics were presented in Simenstad et al. (1982a). During the experiments these fish were fed the three experimental prey species at four different ration levels. All treatments contained five fish per tank except for the high ration levels, which, due to the number of prey necessary to support such high rations, contained two fish per tank. Fish were fed once each day at 14:00 for a period of 8 wk.

The prescribed daily ration levels within each prey category were 1, 5, 10, and 20% of the fish's body weight (% b.w.$\cdot$d^{-1}). Live fish were weighed each week in water-filled weigh plans to update rations. Excess water carried by the fish to and from the balance was estimated by weighing 30 live fish and comparing their live determined weights with their dead wet weights, with excess water blotted away. This produced a correction factor of 0.79 × "live weight," which was applied to experimental fish to estimate dead wet weights. Multiple live weighings of 10 individuals produced coefficients of variation not exceeding 1% and deviations from dead wet weight not exceeding 7%. Since fish were not individually identified, weekly weights were averaged over all fish in a treatment. Prey dry weights were determined by drying large samples of each at 80°C for 48 h, thereby allowing the calculated ration weights to be converted to prey number. Counts of *Tigriopus* and *Pseudocalanus* were estimated using volumetric extrapolation of sample counts from cultures, and *Paramoera* were counted directly. Coefficients of variation for prey counts never exceeded 15%.

To calculate rations, both fish and prey had to be expressed in terms of dry weight, since wet weights of prey proved highly variable and impractical. To estimate fish dry weights, a sample of 30 fish of a wide size range was weighed and then dried at 80°C for 48 h to obtain a conversion factor from wet to dry weight (0.21 × wet weight). We realize that the actual dry weights of the experimental fish would be somewhat different among fish at different ration levels (Brett 1979) but feel that they represent reasonable approximations for ration determination.

The actual rations received by each treatment on a percentage of body weight basis differed from the prescribed ration and were calculated at the end of each week based on the actual fish growth observed in that week. The large difference between actual and prescribed rations for *Tigriopus* was due to an error in the initial dry weight determination for *Tigriopus*.

Otolith Analyses

Juvenile chum salmon for otolith analyses originated from the Washington Department of Fisheries hatchery at Hoodsport, Washington, Beverton Creek egg boxes, and the growth experiments described above. Fish not in the growth experiments were maintained on Oregon Moist Pellets® in seawater holding tanks at Friday Harbor Laboratory. To determine increment periodicity, samples of each stock were sacrificed periodically between March and June, 1981, and were immediately preserved in 95% ethanol or frozen.

Otoliths were removed from each fish and stored on glass slides in immersion oil. The lateral surface of each otolith was ground by hand on a glass plate in a succession of 315 and 600 carborundum grit and immersion oil colloid followed by polishing with 1-μm diamond paste. Otoliths were ground to a plane that included the otolith primordium and were viewed under transmitted light with a Zeiss compound photomicroscope. A standard axis in the posterodorsal quadrant of the otolith was measured with an ocular micrometer at 25×.

Verification of increment[2] periodicity required the identification of reference points in the otolith corresponding to known dates in the life of the fish. Several investigators have demonstrated that recognizable checks may be formed in otoliths in response to specific environmental or physiological events (Pannella 1971; Marshall and Parker 1982). Ten otoliths were examined from fish transferred to seawater only 2 d earlier. Without exception, a distinctly darker daily increment was obvious very near the edge of the otoliths (Fig. 1). Although we cannot be certain exactly what physiological or environmental factors produced this check, it served as a dated reference check from which to enumerate otolith increments in experimental fish. Increments were counted from the very dark increment closest to the otolith primordium (Fig. 2) in a smaller number of specimens sacrificed on seven different dates up to 160 d after hatching. Based on conclusions of Marshall and Parker (1982) for a similar check in sockeye salmon (*Oncorhynchus nerka*) otoliths, we hypothesized that this check corresponded to the date of hatching. Increment counts from these reference points to the edge of the otolith were compared with the actual number of days that had elapsed from seawater transfer or hatching to sacrifice. All increment counts recorded were made by the same reader and represent the mean of at least two counts.

Fish otoliths from the growth experiments were prepared in the same way as others and photographed on a standard axis in the anteroventral quadrant at 1000× after grinding. The photographs were enlarged to a total magnification of 3367× and an axis was drawn along the photographs on which individual increments were measured with calipers. Daily increment widths for each fish were averaged over each week of the experiment to coincide with growth measurements, and this mean daily increment width was averaged over all fish in a treatment, since individuals could not be identified in weekly weighings.

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[2] An individual otolith increment is defined as a thin dark band (discontinuous zone) and a wider light band (incremental zone) when viewed with transmitted light (Mugiya et al. 1981).

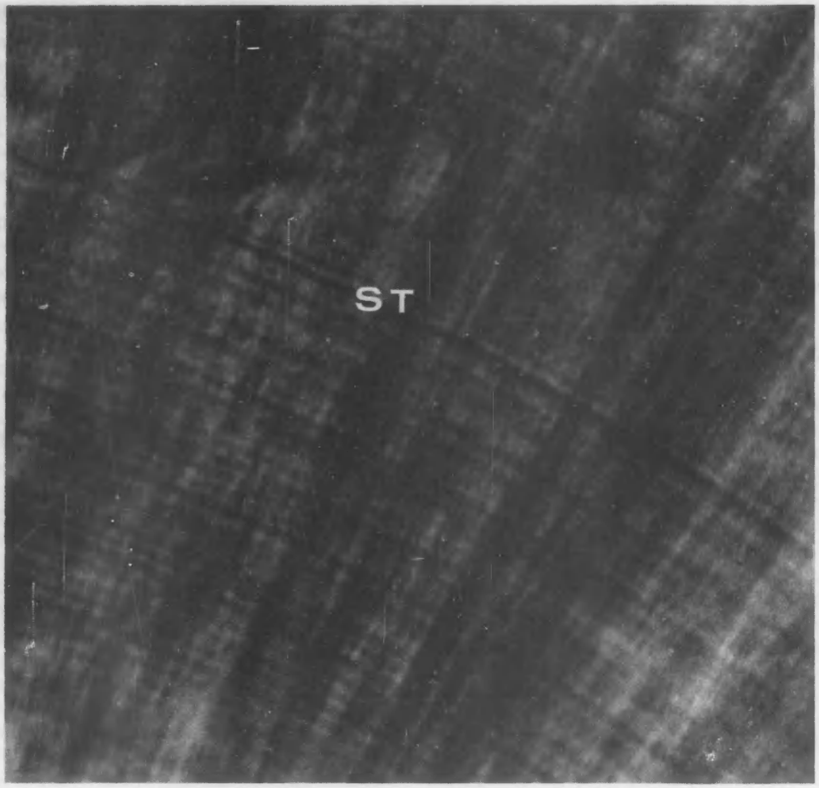

FIG. 1. Seawater transfer check (ST) and daily increments in a chum salmon otolith. Mag. = 1000×.

Results

Fish Growth at Different Prey Rations

Mean fish weights determined weekly for each ration and prey species treatment conformed well to an exponential model for growth ($y = ae^{bx}$) (Ricker 1979). Constant instantaneous growth rates (b) for all treatments ranged from -0.77% b.w. $\cdot d^{-1}$ at a ration of 1.1% b.w. $\cdot d^{-1}$ to 3.37% b.w. $\cdot d^{-1}$ at a ration of 11.4% b.w. $\cdot d^{-1}$. Fish growth within each prey category was significantly different ($P < 0.05$) at each of the four ration levels, and growth rate increased with greater ration in each prey category (Table 1). A more direct comparison of fish growth rates in response to ration level and prey taxa was obtained by plotting fish growth versus ration level or food conversion efficiency ($K = G/R \times 100\%$, where G is growth rate and R is ration received). Fish fed *Paramoera* and *Pseudocalanus* had maximum K values of 16.3 and 20.0% for rations of 9.8 and 9.5% b.w. $\cdot d^{-1}$, respectively, while fish fed *Tigriopus* had a maximum K value of 40.1% for a ration of 5.7% b.d. $\cdot d^{-1}$ (Table 1). Maximum K values for fish in all prey categories occurred at intermediate rations.

Mortalities among low ration fish were common after the 4th wk of the experiment. At the conclusion of the study, four *Paramoera*-fed fish, one *Tigriopus*-fed fish, and all *Pseudocalanus*-fed fish from the lowest ration treatments had died.

Otolith Increments and Reference Checks

The number of otolith increments formed after the seawater transfer check was directly related to the number of days elapsed from placement of fish into seawater to termination of the experiment (Fig. 3, $r = 0.99$, $P < 0.01$). Coefficients of variation for mean counts ranged from 0.3 to 8.6%. Average counts of increments formed after the hypothesized hatching check for fish sacrificed up to 160 d after hatching were also directly related to the number of days elapsed from hatching to sacrifice ($y = 0.94x + 6.70$; $r = 0.96$, $P < 0.01$). Coefficients of variation for these mean counts ranged from 2.2 to 12.4%. Regression analysis over the range of fish sizes examined for all three stocks combined indicated a negatively allometric relationship between otolith radius and fish weight ($y = 404.64x^{0.17}$; $r = 0.92$, $P < 0.05$).

Otolith Increment Width and Fish Growth Rate

Mean daily otolith increment widths for fish grown under the different ration regimes changed little over the course of the experiment. The slopes of these curves were not significantly different from zero with the exception of the low-ration *Paramoera* treatment (Table 2). However, with the exception of the two low-ration *Paramoera* treatments and the two low-ration *Pseudocalanus* treatments, mean otolith increment widths for

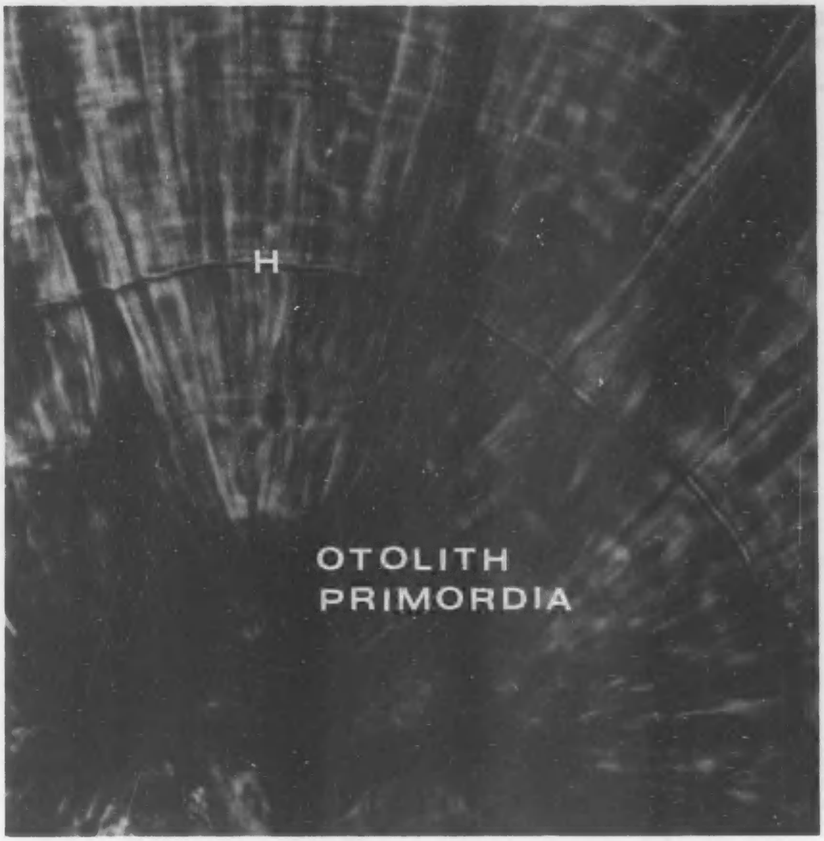

FIG. 2. Hatching check (H) and daily increments in a chum salmon otolith. Mag. = 1000×.

TABLE 1. Mean daily rations, fish weights, conversion efficiencies, and parameters for the exponential growth equation $y = ae^{bx}$, where y = fish weight (g) and x = time (d). Neg. = negative.

Prey	Daily ration ±2 SE (% b.w.·d^{-1})	Time (d)	Initial weight (g)	Final weight (g)	Conversion efficiency (%)	$b(\times 10^{-2})$[a]	a[a]	r
Paramoera	1.9(0.44)	56	0.42	0.28	Neg.	−0.37(0.48)	−0.43(0.16)	0.57
	4.5(0.56)	56	0.65	0.76	11.2	0.50(0.30)	0.74(0.10)	0.82
	9.8(1.02)	56	0.78	1.75	16.3	1.60(0.23)	0.86(0.08)	0.97
	19.3(0.96)	56	0.57	2.70	15.6	3.00(0.19)	0.59(0.06)	0.99
Tigriopus	0.6(0.02)	56	0.50	0.28	Neg.	−0.57(0.24)	0.49(0.08)	0.92
	2.9(0.22)	56	0.60	0.96	35.0	1.00(0.36)	0.66(0.12)	0.94
	5.7(0.24)	56	0.73	2.29	40.1	2.30(0.12)	0.77(0.04)	0.99
	11.4(0.44)	56	0.77	4.50	29.9	3.37(0.24)	0.82(0.08)	0.99
Pseudocalanus	1.1(0.16)	42	0.47	0.37	Neg.	−0.77(0.53)	0.46(0.11)	0.90
	5.0(0.30)	56	0.60	0.73	14.1	0.67(0.15)	0.63(0.05)	0.96
	9.5(0.30)	56	0.64	1.52	20.0	1.80(0.18)	0.65(0.06)	0.99
	18.9(0.96)	56	0.73	2.73	12.7	2.40(0.41)	0.78(0.14)	0.97

[a] ±95% confidence limits.

TABLE 2. Mean daily rations, mean otolith increment widths for the study period, and parameters for the regression $y = bx + a$ of otolith increment width and time for the experimental period, where y = increment width (μm) and x = time (d). NS = not significant.

Prey	Daily ration ±2 SE (% b.w. $\cdot$ d^{-1})	Time (d)	Mean increment width ±2 SE(μm)	a[a]	b[a]	r	N	P
Paramoera	1.9(0.44)	56	1.16(0.24)	1.75(0.20)	−0.13(0.04)	0.96	3	<0.05
	4.5(0.56)	56	1.15(0.12)	1.41(0.20)	−0.06(0.04)	0.84	3	NS
	9.8(1.02)	56	1.73(0.06)	1.81(0.17)	−0.02(0.03)	0.45	3	NS
	19.3(0.96)	56						
Tigriopus	0.6(0.02)	56	1.03(0.08)	1.15(0.16)	−0.03(0.03)	0.62	2	NS
	2.9(0.22)	56	1.33(0.12)	1.54(0.05)	−0.04(0.01)	0.58	4	NS
	5.7(0.24)	56	2.02(0.04)	2.07(0.14)	−0.01(0.03)	0.36	5	NS
	11.4(0.44)	56	2.16(0.04)	2.11(0.01)	0.01(0.01)	0.47	2	NS
Pseudocalanus	1.1(0.16)	42	1.19(0.14)	1.46(0.11)	−0.04(0.03)	0.57	3	NS
	5.0(0.30)	56	1.22(0.04)	1.32(0.01)	−0.02(0.01)	0.74	5	NS
	9.5(0.30)	56	1.83(0.12)	1.92(0.06)	−0.02(0.01)	0.32	4	NS
	18.9(0.96)	56						

[a] ±95 confidence limits.

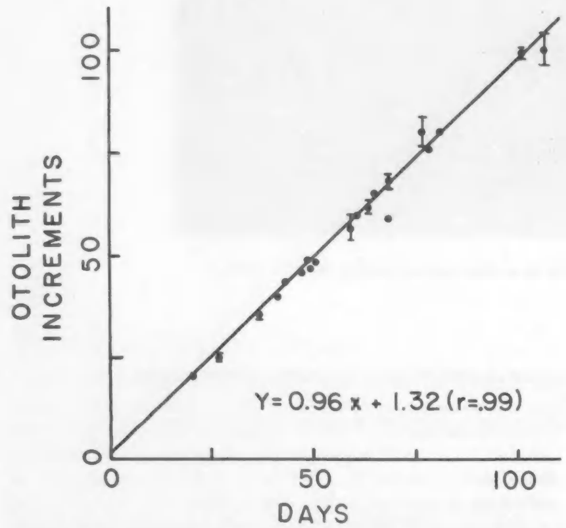

FIG. 3. Regression of number of otolith increments counted from the seawater transfer check against the number of days elapsed from transfer to sacrifice. Error bars = 1 SE.

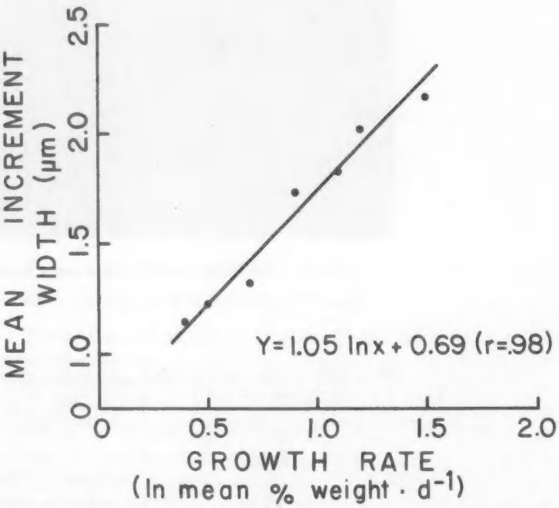

FIG. 4. Regression of mean daily otolith increment width with growth rate (ln (growth rate + 1)) of chum for each treatment. Each point represents the constant instantaneous growth rate and mean otolith increment width for each treatment over the study period.

each treatment within a prey category were significantly different from one another (Table 2, $P < 0.05$). Mean daily increment widths for positively growing fish ranged from 1.15 μm for fish fed rations of 4.5% b.w. $\cdot$ d^{-1} (*Paramoera*) to 2.16 μm at a ration of 11.4% b.w. $\cdot$ d^{-1} (*Tigriopus*). There was a log-linear relationship between mean daily otolith increment width and instantaneous growth rate (Fig. 4, $r = 0.98$, $P < 0.01$) for positively growing fish. Otoliths from the high-ration *Pseudocalanus* and *Paramoera* treatments were not included in this analysis, as preparations were of poor quality. Increment widths for fish experiencing negative growth ranged from 0.7 to 1.5 μm and were similar to those for slow-growth fish.

Discussion

The results of our growth experiments with juvenile chum salmon indicate that fish growth increased with greater daily ration in all prey categories. However, growth rates were generally lower than growth rates estimated in situ (Healey 1979) as well as those reported by LeBrasseur (1969) for juvenile chum feeding on similar rations of planktonic prey (2.2–5.7% b.w. $\cdot$ d^{-1} for rations of 3–17% b.w. $\cdot$ d^{-1}). The much colder water used in our experiments (8–10°C), as opposed to the 14–16°C range in LeBrasseur's, may explain some of the disparity. Reduction in growth of 22–31% for

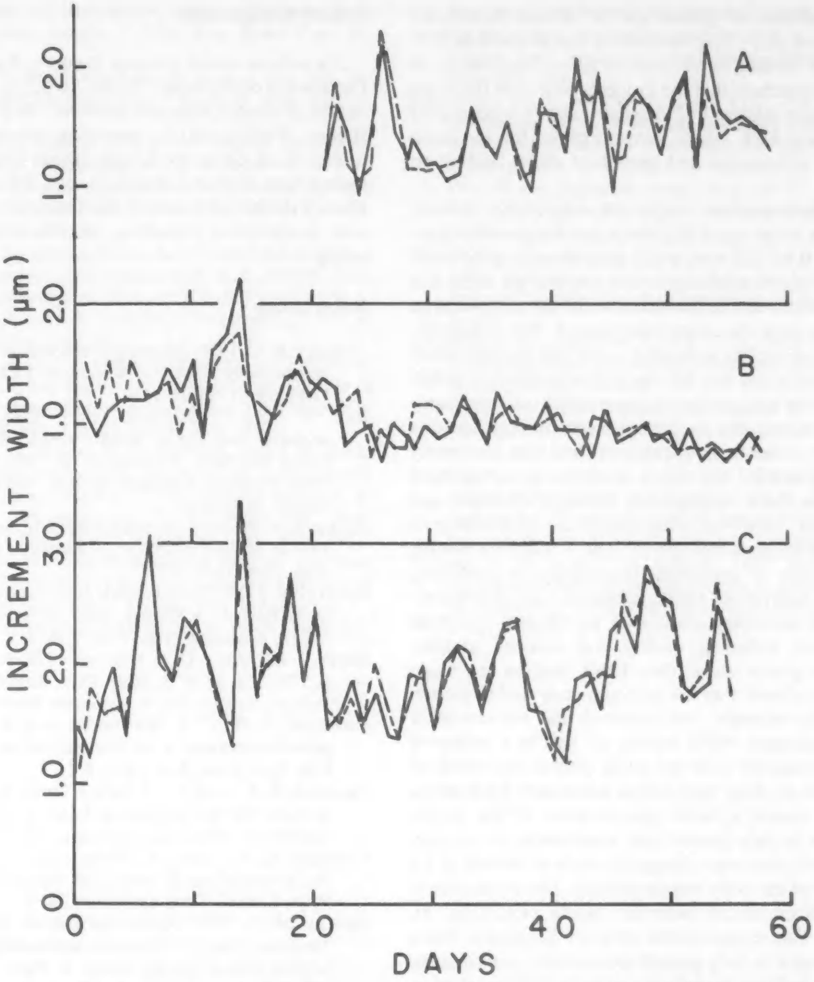

FIG. 5. Daily fluctuations of otolith increment width for three experimental fish. Broken and solid lines represent repeat measurements. Prey and approximate rations are as follows: (A) *Tigriopus*, 3.0% b.w.$\cdot$d^{-1}; (B) *Paramoera*, 4.5% b.w.$\cdot$d^{-1}; (C) *Pseudocalanus*, 9.5% b.w.$\cdot$d^{-1}.

several species of juvenile salmonids reared at 10 versus 15°C has been noted (McCormick et al. 1972; Shelbourne et al. 1973). The relatively small aquaria and the inability of the fish to school may also have retarded fish growth in this study (Brett 1979).

Food conversion efficiencies were much higher for chum fed *Tigriopus* (29.9–40.1%) than for either *Paramoera* or *Pseudocalanus* (11.2–16.3 and 12.7–20.0%, respectively). The values fall within the range reported for other salmonids feeding on natural prey: for brown trout (*Salmo trutta*) feeding on *Chironomus* (43.5%) and on *Gammarus* (15.2%) (Pandian 1967) and for coho salmon (*Oncorhynchus kisutch*) feeding on fly larvae (55%) (Averett 1969). Comparisons with these other studies are difficult, however, because different fish sizes, experimental conditions, and methods of growth determination can produce widely divergent results (Paloheimo and Dickie 1966; Pandian 1967; Chesney and Estevez 1976).

The disparity in food conversion efficiency of fish feeding on the three prey taxa may be explained by comparing the relative energetic benefits of each prey for the fish (Paloheimo and Dickie 1966; Warren and Davis 1967). It has been shown that caloric values for harpacticoid copepods and marine calanoid copepods are at least 35% higher than for amphipods (Cummins and Wuycheck 1971). Amphipods also have a thick, chitinous exoskeleton and may be absorbed less efficiently during digestion than the other prey (Pandian 1967; Brett and Groves 1979). This implies that copepods may return more energy per gram of ingested ration than amphipods. Furthermore, in concurrent chum feeding studies, we have observed that the percentage of successful prey capture attempts by chum on *Tigriopus* was much higher than that with *Pseudocalanus* or *Paramoera* (unpublished data), indicating that *Paramoera* and *Pseudocalanus* have more highly developed escape responses than *Tigriopus*. Vinyard (1982) provided evidence that the energetic expenditure of yellow perch (*Perca flavescens*) consuming evasive prey (*Diaphanosoma*) was as much as 55% higher than when feeding on nonevasive prey (*Diaptomus*). In light of this, we conclude that the low energetic cost for chum capturing *Tigriopus* relative to *Paramoera* and *Pseudocalanus* and their relatively high caloric return explain the increased food conversion efficiencies and growth of chum feeding on *Tigriopus*.

Our investigations confirm a log-linear relationship between otolith increment width and fish growth rate for juvenile chum salmon between 0.60 and 4.50 g and growth rates up to 3.4% b.w.·d^{-1}. The same relationship results whether the mean fish growth rate and mean otolith increment width are calculated on a weekly basis or over the entire study period. The nonsignificance of all but one otolith increment width plot over the study period (Table 2) indicates that fish size had little effect on otolith increment width for fish growing at these rather constant rates.

Although the notion that otolith microstructure can predict fish growth rate is not a new one, we feel that this study represents a step toward defining a relationship during short intervals such as their outmigration through estuarine and nearshore habitats. However, even though the relationship of otolith increment width to fish growth rate is valid for weekly mean values, there is increasing uncertainty in predicting growth rates for intervals of shorter duration. Calcium deposition and resultant increment width may be affected by a wide variety of factors including quality and quantity of diet, temperature, and photo period (Irie 1960; Neilson and Geen 1982), and these effects may not be completely tied to growth rate changes. For example, we observed that while weekly mean otolith increment width among all fish in a treatment remained fairly constant over the study period, the width of otolith increments in chum may exhibit large daily fluctuations (Fig. 5). If we accept a literal interpretation of the otolith increment width to fish growth rate relationship on a daily resolution, growth rates may change as much as 14-fold in 1 d and exceed 10% of the body weight per day. Since variation is low in our replicate otolith increment width plots (Fig. 5), influences other than experimental error are suggested. Since such radical changes in daily growth are unlikely, environmental and physiological factors probably influence calcium deposition to otoliths in ways not reflected in fish weight changes. It is also important to note that the relationship of otolith increment width to fish growth rate was based on experiments with fish grown at rather constant rates. Because physiological condition of the fish will likely influence the deposition of calcium to the otoliths, similar growth rates in fish of different physiological "histories" may be represented differently in otolith microstructure.

In summary, there is increasing evidence that early marine survival of juvenile chum is related to their size at outmigration (Parker 1971; Healey 1982). These findings underscore the adaptive significance of estuarine residence for juvenile salmon, where rapid growth rates are characteristic and potentially enhance marine survival. A more thorough understanding of the biological and physical processes that affect individual growth and production of juvenile chum salmon in estuaries still remains a central goal of fisheries research. This study provides a basic link towards this end by illustrating a potentially powerful methodology that can easily be applied to in situ determination of estuarine and early marine growth of chum without expensive, complicated mark and recapture experiments.

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Influences of Stock and Site on Growth and Mortality in the Blue Mussel (*Mytilus edulis*)

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Dickie, L. M., P. R. Boudreau, and K. R. Freeman. 1984. Influences of stock and site on growth and mortality in the blue mussel (*Mytilus edulis*). Can. J. Fish. Aquat. Sci. 41: 134–140.

Reciprocal transfers of three blue mussel (*Mytilus edulis*) stocks among three rearing sites resulted in marked changes in growth, mortality, and maximum biomass. Results indicate that site differences were major determinants of the growth effects, while stock differences were chiefly responsible for the mortality effects. The overall effect on biomass and potential yield was approximately equally attributable to site and stock influences. The results have relevance to aquaculture and environmental assessment using mussels and illustrate genotypic responses that may be significant for fisheries management.

Des transferts réciproques de trois stocks de moules (*Mytilus edulis*) entre trois sites d'élevage ont entraîné des variations importantes de la croissance, de la mortalité et de la biomasse maximum. Les résultats révèlent que les différences entre les sites ont constitué des déterminants majeurs de la croissance tandis que les différences entre les stocks ont été en grande partie responsables de la mortalité. L'incidence globale sur la biomasse et le rendement potentiel a été à peu près à parts égales attribuable au site et au stock. Les résultats sont significatifs pour l'aquiculture et les évaluations environnementales qui utilisent des moules et illustrent des réactions génotypiques qui peuvent être importantes pour la gestion halieutique.

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Differences in biomass and production of organisms result from changes in both the short-term physiological responses of individuals to environmental perturbation and the longer term genotypic responses of populations to average environmental patterns. It is of increasing practical importance to determine the balance between these two major classes of influence. In fisheries, for example, we are beginning to recognize that although maximum sustained yield is affected in the short term by fishing intensity, in the long term it can be influenced by the selective action of certain gears or fishing strategies on the breeding populations. In aquaculture, while environmental factors have important effects, genotypic differences offer the potential advantages already demonstrated in agriculture by a long history of deliberate selection and development of stocks. In environmental assessment, attention is generally focussed on immediate response, but subsequent adaptation by populations may be an equally important part of the solutions sought by management.

The balance of short-term and long-term responses may differ markedly among situations and organisms. Gause (1947) showed reciprocal relationships between the two classes of adaptative mechanisms and suggested that gradual changes in the average level of environmental conditions may result in a higher proportion of the total adaptation appearing in the genotype, while environments with significant fluctuations around an environmental mean may favor mechanisms for physiological adaptation. Since then, much has been learned about heritability in terrestrial species, but marine systems differ from terrestrial in the scales and degrees of environmental change. On both pragmatic and theoretical grounds it is questionable whether evidence from terrestrial systems provides an adequate basis for judging the relative importance of genetic and environmental response mechanisms in life history strategies of marine organisms.

In this paper we report the results of experiments explicitly designed to measure the relative importance of stock in the phenotypic response of production parameters in a marine species. Samples of wild populations of blue mussel (*Mytilus edulis*) were taken from three localities within the Maritime Provinces and reciprocal transfers were made among them in three successive years. Isoenzyme analyses showed that there were significant differences in genetic constitution among the three stocks (Gartner-Kepkay et al. 1980). Observations of growth and mortality were made at frequent intervals, and in the analysis we partition the variances between short-term environmental or site influences and the longer term stock influences.

Methods

Experimental Design

Two of the three sites, St. Margarets Bay and Bedford Basin, are on the Atlantic coast of Nova Scotia. The mussels were taken from near the two rearing sites used by Freeman and Dickie (1979). The third site was in the Gulf of St. Lawrence, at Ellerslie, on the western shore of Malpeque Bay, Prince Edward Island. As pointed out by Gartner-Kepkay et al. (1980) in the study of the isoenzyme composition, the first two are relatively stable environments while the Ellerslie site shows seasonal extremes, with warm summer temperatures, ice-covered winter conditions, and highly variable salinity throughout the year. Mussels were taken from below low-tide mark at all three localities.

In each experiment, samples of mussels were collected, cleaned, and for a short period held near the surface in cages to permit culling of dying or aberrent individuals. Each stock lot was then divided into three groups, one for rearing in its native area and two for transfer to the other sites. Stock groups were placed in separate ample cages made of 10-mm rigid plastic mesh and suspended about 1 m below the surface from rafts moored in relatively open water. The first triple transfer was made in June 1976. Repeat transfers were made in June 1977 and August 1978.

In the 1976 and 1977 stock transfers, mussels were confined to two size classes, 40 ± 2.5 and 50 ± 2.5 mm total shell "length." Twenty-five animals were selected in each size category for separate rearing at each site, giving a total of 150 animals in six cages at each site. Each animal was individually identified by a number and each lot was observed once a month, at which time individual lengths (to the nearest 0.1 mm) and mortalities were recorded and the cages were cleaned and replaced. In 1978, two size groups of 50 mussels each were initiated; the first, consisting of mussels comparable to the 40-mm size class started in 1976 and 1977 and the second consisting of 15 ± 2.5-mm mussels, raising the starting number to 300 at each site. Growth rates were calculated for each individual mussel in terms of change in length between measuring dates, expressed as annual instantaneous rate of growth (Ricker 1975). Preliminary analysis of results from the first two transfer experiments showed that growth rates and variances were such that the original 40- and 50-mm size groups were statistically indistinguishable. We decided to treat them as replicate samples so that we could derive a "within-treatment" component in the estimates of mortality rates. To carry out comparable mortality rate analysis for the 1978 transfer we divided the initial size groups of 50 animals into replicate groups of 25 animals each. The ratio of the number of animals dead at the end of the observation period to the initial numbers for that period was used to calculate annual instantaneous mortality rate. In the analysis of both growth and mortality rates, average values for growth in length and mortality in numbers are determined for each observation period for each initial starting group of 25 animals. These are the basic data employed throughout the analyses.

Biomass calculations require estimates of growth and mortality in terms of weight. Weight of mussels present at a given time was determined by interpolating the length of each of the survivors in a group between measuring dates and converting length to weight using the relation $W = a \times l^b$ where W and l are wet meat weight and total shell length, respectively, and a and b are empirically derived constants. In our calculations we used the values $a = 2.63 \times 10^{-5}$ and $b = 2.65$, which are averages from numerous earlier seasonal measurements at several sites. Biomass is defined as the sum of the calculated weights of all survivors in a group.

Analytical Methods

Our primary analytical tool is the classical analysis of covariance, for which we utilized the default options in the ANOVA programs available through SPSS (Nie et al. 1975). Throughout the analysis we lumped all three-way and higher interaction with the residual error term. These programs were used to evaluate the contribution of several variables to the total observed variance in growth, mortality, and biomass. In addition to aggregation by stock and site; season, calendar year, and experimental year were defined and tested for significance with the aid of the ANOVA programs. Covariates of length and weight were used throughout to remove the "age" trends in the dependent variables. Weighted means produced by these programs were used for regression analysis and prediction of biomass.

Growth and mortality are not distributed evenly throughout the year. In an earlier experiment, with relatively small numbers observed, Freeman and Dickie (1979) divided the year into two parts: a warm- and a cold-water season of 6 mo each. In these experiments, involving observtion of three transfers over about 2 yr each, growth and mortality were not homogeneously distributed within 6-mo periods and such periods were not the same at different sites. Accordingly, we examined the merits of using different definitions of season. ANOVAs of growth and mortality were carried out using seasons of 6, 4, 3, and 2 mo duration. The results established the fact that for both growth and mortality, four seasons of 3 mo each per year gave the highest ratios of the "between-season" to "within-season" variations, hence highest "within-season" homogeneity. For at least the mortality data, it also appeared that while there was some apparent variation in the date of onset of the high summer mortalities, the 3-mo period of June 15–September 15 included most of it. Accordingly, we set up a sequence of 3-mo seasonal periods: June 15–September 14, September 15–December 14, December 15–March 14, and March 15–June 14 for all sites and years.

Experiments began in mid-June of 1976 and 1977; however, logistical problems delayed the 1978 experiment until August. From the beginning date, monthly observations on each lot were made for at least 24 mo unless mortality rates reduced the number of survivors to zero. In an effort to minimize asymmetries in the ANOVA, calendar year was incremented at the beginning of the September season and incomplete calendar years were excluded from analysis of the calendar year variable. Observations are thus available for only one complete calendar year for each of the first two experiments. The 1978 experiment, which began late, was continued until November of 1980, providing data for two calendar years. That is, data are available for four consecutive calendar years of four seasons each.

Each experiment ran for about 2 yr, thus we were able to test for effects of duration in the cages, beyond those implied by the covariates defined below. In a special ANOVA the data for each experiment were divided into two nearly equal parts called "experimental years."

Length is the strongest predictor of growth rate and is in general used as an indicator of metabolic processes related to body size or age. In the analysis of growth rates, length is therefore an obvious covariate. This and previous analysis (Freeman and Dickie 1979) show that mussel growth rate is a curvilinear function of length. Because our interest is in production processes related to the metabolism of the entire biomass, we decided to correct for this curvilinearity by supplementing the linear covariate with another that would reflect weight changes. As the second covariate we used the weight term as calculated above. The covariates length and weight have statistically significant effects on growth, mortality, and biomass although, as might be expected, their effects are greatest on growth.

Freeman and Dickie (1979) concluded that persistence of growth rate within individuals signified an effect of genotype on growth. Here, we checked for the continuing presence of growth patterning by the use of Kendall's measurement of

TABLE 1. ANOVA for growth, mortality, and biomass.

	Growth			Mortality		Biomass	
Source of variation	Degrees of freedom	Mean square	Significance	Mean square	Significance	Mean square	Significance
Covariates	2	11.45	0.001	5.24	0.005	12 150.3	0.001
Length	1	6.13	0.001	10.48	0.001	23.2	0.378
Weight	1	1.78	0.001	9.82	0.001	1 266.6	0.001
Main effects	7	1.20	0.001	34.64	0.001	1 425.1	0.001
Stock	2	0.59	0.001	27.16	0.001	2 729.3	0.001
Site	2	2.14	0.001	20.38	0.001	2 189.0	0.001
Season	3	0.95	0.001	50.92	0.001	114.6	0.010
Two-way interactions	16	0.10	0.001	12.12	0.001	45.4	0.087
Stock–site	4	0.09	0.002	4.80	0.001	110.7	0.005
Stock–season	6	0.18	0.001	13.69	0.001	39.1	0.251
Site–season	6	0.04	0.093	15.95	0.001	7.8	0.955
Explained	25	1.32	0.001	17.88	0.001	948.9	0.001
Residual	504	0.02		0.96		29.8	
Total	529	0.08		1.76		93.9	
Multiple R^2			0.727		0.272		0.690
Multiple R			0.852		0.521		0.830

concordance. Growth of individuals within each stock lot was ranked, and rankings for each lot were compared between seasons over the experiment. The tests confirmed a highly significant concordance of growth patterns. In addition to strong persistence in individual growth means, their variance remained almost constant with time.

Results

Growth Rates

Analysis was begun by classifying the data to reflect the influence of four main effects: stock, site, season, and experimental year. There was no significant effect of experimental year, a conclusion that supports our a priori decision to use length and weight as covariates to normalize mussel growth for the age of the animals and that dismisses any concerns about cage effects. When calendar year was substituted for experimental year, the multiple correlation coefficient was 0.87, but the variance accounted for by calendar year was less than 3% of the total. In fact, two-way interactions of calendar year with both season and site were greater than its apparent main effect. Such interactions are to be expected: there will be differences in seasons between calendar years, as well as year-to-year differences between geographical locations that are several hundred kilometres apart. Since the interaction of stock with calendar year was not statistically significant and arrangement of the data into symmetrical calendar years had reduced our total available data points by 20%, this classification was also dropped. Without it, the overall correlation coefficient was 0.85, accounting for 73% of the variation, further evidence of the relative unimportance of calendar year on growth rates over the 4-yr period of observations.

In the final analysis of the growth data (Table 1), site differences appear as the dominant factor, being about twice as important as the seasonal differences, which are evident in all levels of general animal activity in our coastal environment. The weighted growth means derived from the analysis (Table 2) indicate that the component due to site principally reflects the slow growth at the Ellerslie site. Growth there averaged 60% below the general mean, while growth at the two sites on the Atlantic coast, Bedford Basin and St. Margarets Bay, was nearly uniformly 30% above the general mean.

TABLE 2. Multiple classification analysis. Means and ranges of the classification averages and the grand mean are adjusted for variable and covariates.

	Growth		Mortality		Biomass	
Variable and category	Mean	Range	Mean	Range	Mean	Range
Grand mean	0.24		0.55		14.8	
Stock						
Ellerslie	0.30		0.13		19.7	
Bedford Basin	0.20		0.83		11.5	
St. Margarets Bay	0.22	0.10	0.71	0.70	12.9	8.2
Site						
Ellerslie	0.09		0.85		12.0	
Bedford Basin	0.32		0.56		13.3	
St. Margarets Bay	0.31	0.23	0.23	0.62	19.2	7.2
Season						
June 15–Sept. 14	0.24		1.70		16.6	
Sept. 15–Dec. 14	0.28		0.33		14.1	
Dec. 15–Mar. 14	0.12		0.17		14.1	
Mar. 15–June 14	0.35	0.23	0.27	1.53	15.0	2.5

Stock makes a contribution to total growth variance that is only about two-thirds as important as the seasonal effect. Since our experimental designs permitted us to examine "adult" growth of the three stocks under closely parallel conditions at all three sites, this stock effect may be considered as an index of the effect of genetic constitution on growth variance. The adjusted means (Table 2) show a 30% higher growth performance by the Ellerslie stock over all sites compared with the average performance of the Bedford Basin and St. Margarets Bay stocks at 20 and 10% below the mean.

Two-way interaction terms, while statistically significant, are generally small compared with the main effects (Table 1, growth). The most important two-way interaction is the one between stock and season, indicating that not all stock growths were equally sensitive to the effects of seasonal change. There is also an indication in the significant stock–site interaction term that there is no totally unique way of defining a stock without taking features of its environment into account. The small scale of these interactions indicates that the mean squares for the main effects give a reasonable measure of their relative importance in the total growth variance.

Mortality Rates

As with the growth data, experimental year explained none of the variance in mortality (Table 1). Similarly, analysis of the data by calendar years revealed that F ratios involving it were smaller than comparable values for the growth data, the main effect being barely significant at the 5% probability level, while interactions involving it were even smaller. The overall correlation coefficient of 0.52 indicates that stock, site, and season accounted for 27% of the total mortality rate variation.

The major contrast between the mortality analysis and the growth analysis is the marked reduction in the influence of site, which in this instance explained only about half as much of the variance as did the seasonal classification. On the other hand, the stock classification appears to have about the same importance relative to season as was revealed in the growth study.

In the mortality analysis, interpretation of the main effects is less certain than in the growth study for two reasons: the much reduced multiple correlation coefficient and the relatively larger interaction terms, particularly those involving season. We realized at the outset of the experiments that for mortality measures we were using minimal numbers in our observation groups. However, the low correlation coefficients are not simply a reflection of small sample size. They also reflect the idiosyncratic seasonal patterns of mortality. To arrive at a level of aggregation that would best characterize the data we examined the nature of this basic variation in some detail. We found that if within the 3-mo seasons each group of mussels was divided into two half-groups (of 13 and 12 animals each) there was no change in the F ratios for the tests. However, if the observation period was shortened to 1.5 mo, the variance was markedly increased. That is, a major fraction of the mortality variance is apparently attributable to uncertainty in the time at which mortality occurred rather than an overall difference in susceptibility of the group members to mortality. Lengthening the defined season beyond 3 mo decreased the within-season variation but also obscured some of the seasonal biological sequences. We therefore maintained the seasonal definition even if it slightly reduced the sensitivity of estimation of the stock and site main effects. The overall analysis leaves little room to doubt either the reality of the influence of the three main effects or the major difference in the apparent influence of stock and site on mortality, compared with the affects on growth.

Both the data plotted in Fig. 1 and the adjusted mean values derived from the ANOVA (Table 2) suggest that mortality is at least as important as growth in the overall dynamics of mussel production. For example, the Ellerslie stock showed a 30% higher average growth rate, and its overall mortality rate was 75% below the general mean. Differences in mortality of the Bedford Basin and St. Margarets Bay stocks were also large in comparison with growth, being 50 and 25% above the general mean, respectively. Similarly, there were substantial differences in growth and mortalities between sites. Growth rates at the two coastal sites were about equal, whereas mortalities at Bedford Basin were 2% above average and those at St. Margarets Bay 60% below it. The Ellerslie site, which showed an overall 60% mean growth retardation, suffered a corresponding mortality increase of nearly 60%. Evidently, while growth and mortality are affected by both stock and site, the average impacts of growth and mortality are neither the same nor always of the same relative importance as determinants of the overall stock dynamics. Genetic and environmental influences appear to have different relative impacts on the stocks at different localities.

Biomass Differences

Biomass is the result of the interaction of growth and mortality on a given cohort. In these experiments different initial starting sizes were chosen to allow observations of interaction over a total life history of about 4 yr. The ANOVAs indicated that biomass has to be predicted separately for each stock and site. Calculated biomasses for each of the three stocks at each of the three sites, beginning with the equivalent of 15-mm animals, and modeled seasonally over a 4-yr period, are shown in Fig. 2. Also shown are calculated growth curves in length and calculated numbers surviving.

The most striking feature is the outstanding biomass development of the Ellerslie stock at all sites. This contrasts sharply with the low performance of the two stocks introduced into the Ellerslie site. The observed difference is in keeping with conclusions of experienced shellfish growers that the best seed stock comes from the "toughest" environment. The Ellerslie site clearly represents a tough environment, and the Ellerslie stock appears admirably suited to succeed in it.

It is an interesting and possibly important observation that the advantages of the exceptional hardiness of the Ellerslie stock are enhanced when it is transplanted to the coastal oceanic sites where its high rate of survival combined with its higher initial growth results in higher biomass at all ages than was attained by the other stocks. This resulted in a higher biomass development in the coastal areas than it sustained in its native environment.

These data are indications of the importance of genetic factors as determinants of the population dynamics of the mussel. We show in Table 1 the results of the analysis of covariance. The seasonal effect is small when the data are treated in this fashion; so too are all of the interactions. The mean squares under the main effects of stock and site indicate that these two are overwhelmingly important, with effects of stock somewhat predominant over effects of site. The analysis explained 69% of the total variation in biomass.

Discussion

The results show that the source of mussel stocks strongly determines the production parameters underlying adult biomass. It affects the average level of the growth and mortality parameters, their degree of variation, and the time sequences of changes in them during the life history of cohorts. Highest average stock growth was of the order of 1½ times that of the lowest stock growth; highest average stock mortality rate was over 6 times the lowest. Initial maximum growth rate for the experimental groups ranged from 0.25 to 0.85 and the time of its major asymptotic inflection differed by as much as 2 yr. Differences in mortality rates of 3- and 4-yr-olds were generally greater than those of 1- and 2-yr-olds, and the seasonal maximum in mortality occurred at different times and and at different ages among stocks and sites. Despite these wide ranges

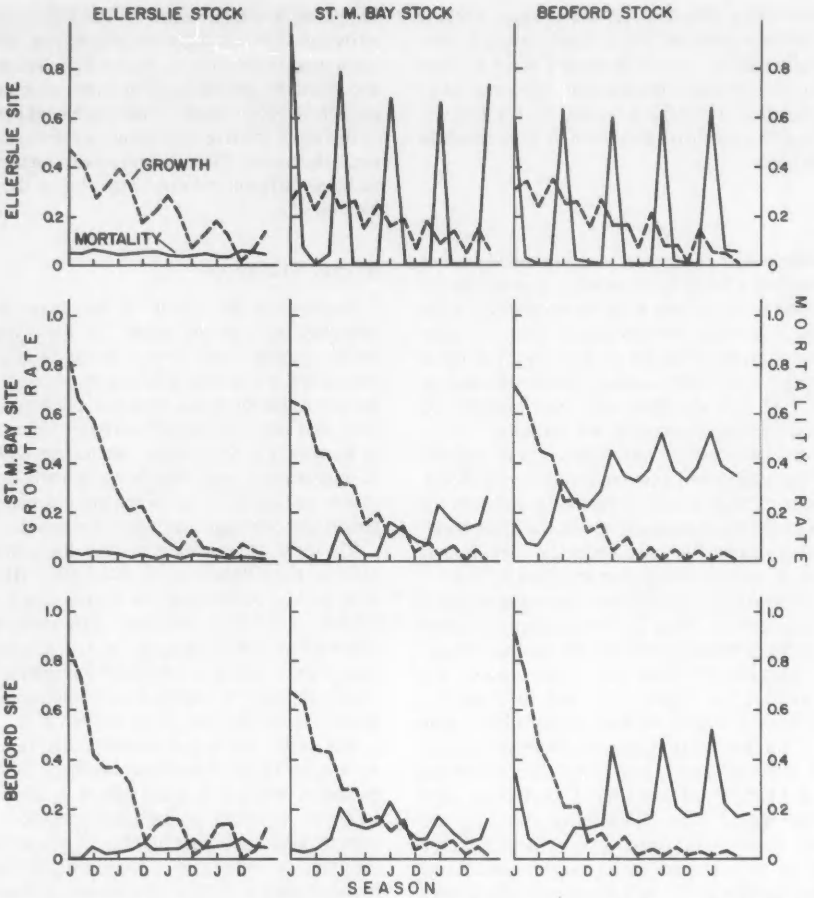

FIG. 1. Annual instantaneous growth and mortality rates of the mussel samples by stock, site, and season.

in the parameters, the relative biomass attained by the stocks in their native habitat showed only a threefold range, suggesting that there are compensatory interactions in natural production systems. By contrast, interaction of stock with site in mussels transferred to new sites gave rise to striking effects. Maximum biomass development of the hardiest Ellerslie stock, when transferred to St. Margarets Bay, was of the order of 17 times that of the lowest biomass development that occurred in the St. Margarets Bay stock transferred to Ellerslie.

The significance of source stock, hence of genetic constitution, is difficult to quantify but some further appreciation of relative importance may be made by comparing the effects of stock with those due to site and season (Table 2). For the growth data, the range of the seasonal and site means is equivalent to the magnitude of the overall mean, while average growth differences among stocks were only of the order of one-third the overall mean. In the mortality data, seasonal variations were 3 times greater than the overall mean, while differences in the average mortality level for stocks and sites were about 1¼ times the mean. That is, differences in growth and mortality due to stock are generally of the order of expected seasonal and site variations, although the effect of site (environment) is relatively more important for growth, while the effect of stock (genetics) is more important for mortality. A similar conclusion has been reported for the oyster (*Crassostrea virginica*) by Mallet and Haley (1983).

In judging the general significance of the stock and site differences, it should be noted that the Ellerslie site was chosen partly because differences between it and the coastal sites represent close to the maximum range of environments within the Maritimes region. The fact that the stock effect was of the same order as the site differences provides some perspective. Genetic constitution clearly has a practical impact on marine production.

The interpretation of the mortality results appeared initially to be complicated by the markedly poor performance of coastal stocks introduced into the Ellerslie environment. Superficially, this pattern of behavior was reminiscent of the aggregate behavior of mainland oysters that had been introduced into the Ellerslie site in the 1940's following the history of recovery of local stocks from the "Malpeque" disease, which had devastated the oyster industry of the region (Needler and Logie 1947). Recently, among blue mussels of Prince Edward Island that were suffering a high January mortality, Li and Clyburne (1979) identified a disease organism similar to that found in affected oysters. However, while our introduced animals suffered high mortalities, it is notable that high mortality occurred in summer, when they suffer mortalities in their home environments (Fig. 1)

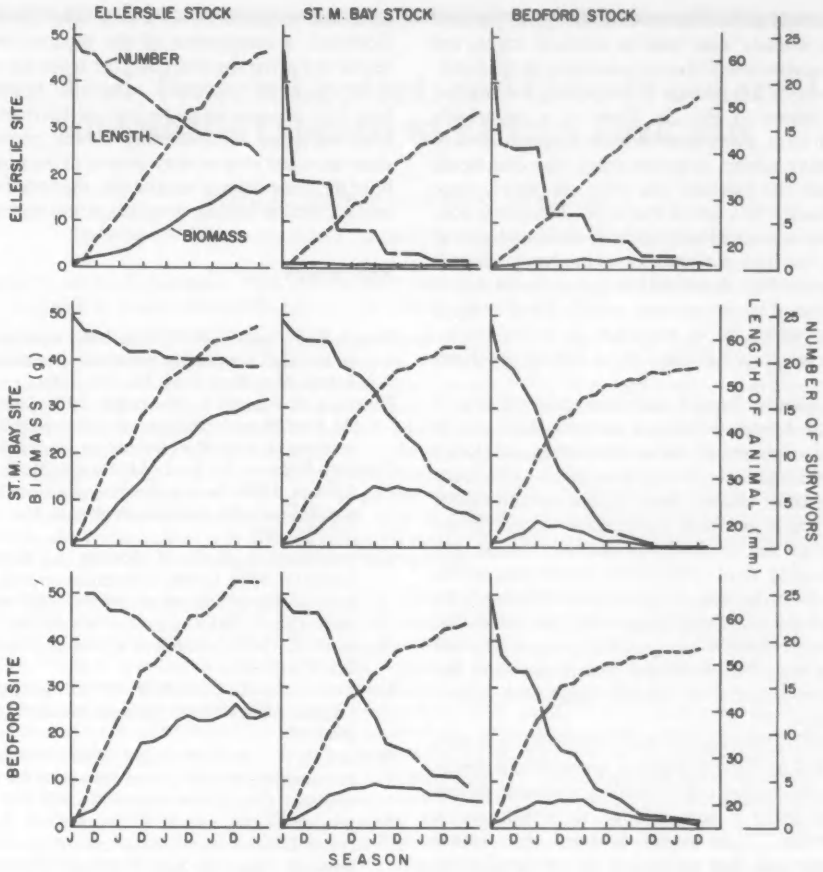

FIG. 2. Calculated seasonal average size (total shell length), number of survivors, and average biomass of each initial sample of 25 animals by stock and site.

and that mortalities of Bedford Basin stock were nearly as high in their native area as in Ellerslie. Since the oyster disease and its apparent counterpart in mussels are a late fall and winter phenomenon, we concluded that whatever the cause of the higher mortality of the Nova Scotian coastal stocks in Ellerslie, it did not appear to have been an encounter with the oyster disease. In fact, the parallelism with mortality patterns in their home environments supports the inference that there is a genetic basis for the mortality pattern.

The impact of selection for mortality resistance on yield has been pointed out by Doyle and Hunte (1981) who reported a mortality reduction of 50% and a threefold yield increase by a laboratory population of *Gammarus* selected for fitness to the laboratory environment over only 26 generations. The potential importance of genetic selection for resistance to mortality as a determinant of production in mussels is reflected here in the differences in biomass of the transferred stocks (Fig. 2). The coastal mussel stocks, from St. Margarets Bay and Bedford Basin, are clearly not attuned to the highest possible adult biomass production in their native habitat, although each of them did best when reared there. This evidence suggests a tendency towards different genetic equilibria even in continguous embayments. The difference in biomass response of the transplanted Ellerslie and coastal stocks indicates something of the scope for genetic adaptation by postlarval mussel stocks.

It is clear from the differences among transplants that there are unequal contributions of phenoadaptation and genoadaptation to the determination of biomass. For example, the St. Margarets Bay and Bedford Basin stocks showed markedly lower biomasses when transferred to Ellerslie, while the reciprocal transfers gave biomass enchancement of the Ellerslie stock. These responses to transfer indicate a relatively low capacity of the mussels for short-term physiological adaptation. On the other hand, the superior performance of the Ellerslie stock in all situations is an index of its prior genoadaptation to the apparently tough environment in which it has evolved. Since the mussel shows such an apparently low physiological adaptability, it would appear to be useful as an indicator of local environmental perturbation. By contrast, because of the apparently strong genoadaptation, comparisons of the production of native mussels in different areas is a poor basis for indexing environmental difference. The apparently strong capacity for genoadapation by mussels may account for their ubiquity in coastal marine ecosystems.

Blue mussels are an object of growing interest to aquaculture, and our results are of clear significance to aquaculture practices.

While our data do not permit us to estimate yield per unit growing area, the animals were held in identical cages, and hence, relative biomasses should be representative of productivity and relative commercial yield can be indexed by the biomass and length data shown in Fig. 2. There is a remarkable difference between sites, even when indexed by production of mussels in their native habitat. A grower using such data would be likely to choose the Ellerslie site over all others, since potential yield is nearly 50% above that of St. Margarets Bay, albeit the maximum is reached only after an additional year of growth. However, the high performance of the hardy Ellerslie stock in St. Margarets Bay shows that an aquaculturist free to choose a combination of stocks and sites would clearly be much better off than he would be if restricted to native stocks. Artificial selection might well enhance these differences (Newkirk 1980).

The factors accounting for the improved performance of Ellerslie stocks in St. Margarets Bay are not well understood at present. As a partial explanation, the results of Peterson (1980) suggested that Ellerslie mussels have a higher grazing efficiency than those from the other environments. If this is confirmed, it would appear that genetic selection for nutrition-related factors may play an important role in mussel productivity. Isoenzyme studies (Gartner-Kepkay et al. 1983) have shown that stocks from the estuarine Ellerslie site are genetically different from those in the coastal sites, although they resemble stocks that exist at headwater sites in the St. Margarets Bay region. It is not yet known whether these "head-of-inlet" stocks also show the superior aquacultural potential of Ellerslie stocks, but experiments are in progress.

Finally, the mussel results suggest that genetic selection may need to be taken into account in fisheries management generally. For example, in commercial fisheries assessment, where sampling problems make it very difficult to obtain precise extimates of mortality, it is usually assumed that natural mortality is constant and that yields can be predicted from changes in growth and fishing intensity alone. Fisheries increase the mortality rate of the populations, and various gears and strategies exert strong size-selection. Both markedly alter the size and age structure of the breeding stocks and change their genotypes. If heritability of production parameters in fish resembles that of mussels, Table 2 and Fig. 2 illustrate the response of fish populations to fishing on both short-term and long-term time scales. For example, the effects on biomass and yield of the transfer of mussels from a favorable to an unfavorable environment are analogous to the short-term impact of an increase in mortality due to fishing. In our experiments this gave rise to as much as a threefold change in production. However, a comparison of the biomass of different stocks reared at a given site illustrates the scope for production change as a result of continued selection pressures. Comparable long-term changes might be expected in marine animal populations subjected to continuing fishing pressure. Because the short-term and long-term responses of the populations appear to be of the same order of magnitude, they need to be taken equally into account in setting up management regimes.

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Nucleic Acid, Protein Content, and Growth of Larval Fish Sublethally Exposed to Various Toxicants

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Barron, M. G., and I. R. Adelman. 1984. Nucleic acid, protein content, and growth of larval fish sublethally exposed to various toxicants. Can. J. Fish. Aquat. Sci. 41: 141–150.

Larval fathead minnows (*Pimephales promelas*) were exposed for 96 h to several concentrations of benzophenone, ethyl acetate, hexavalent chromium, hydrogen cyanide, or *p*-cresol. The range of "safe" concentrations determined from 96-h macromolecular content (RNA, DNA, and protein) and growth was within or very near the range of "safe" concentrations determined by concomitant longer term exposure (28- to 32-d early life stage toxicity test). RNA, DNA, and protein content per larva and RNA/DNA ratio were sensitive to toxicant stress and followed a log-linear dose response. Larval RNA content appeared to be the 96-h measurement most responsive to toxicant exposure. A disruption of nucleic acid and protein metabolism apparently occurred within 96 h of sublethal toxicant exposure and resulted in (1) decreased rates of mitosis, (2) reduced protein synthesis, and (3) reduced growth. Measurement of growth and macromolecular content after a 96-h larval exposure provided a physiologically relevant measurement of toxicity that was predictive of longer term sublethal toxicity.

Des larves de tête-de-boule (*Pimephales promelas*) ont été exposées pendant 96 h à plusieurs concentrations de benzophénone, d'acétate d'éthyle, de chrome hexavalent, d'acide cyanhydrique ou de *p*-crésol. Les concentrations "sécuritaires" déterminées à partir du conténu macromoléculaire après 96 h (ADN, ARN et protéine) et de la croissance se situaient dans la gamme ou très près de la gamme des concentrations "sécuritaires" déterminées par une exposition simultanée à plus long terme (test de toxicité de 28 à 32 jours pour les premiers stades de développement). Le contenu en ARN, en ADN et en protéine par larve ainsi que le rapport entre l'ARN et l'ADN étaient sensibles au stress des substances toxiques et suivaient une réponse linéaire logarithmique des doses. Le contenu en ARN des larves a semblé être la mesure de 96 h la plus sensible à l'exposition aux substances toxiques. Une perturbation du métabolisme des acides nucléiques et de protéines s'est produite apparemment en moins de 96 h d'exposition sous-létale aux substances toxiques, ce qui a entraîné (1) une baisse des taux de mitose, (2) une diminution de la synthèse des protéines et (3) une réduction de la croissance. La mesure de la croissance et le contenu macromoléculaire après une exposition de 96 h des larves ont fourni, au point de vue physiologique, une mesure pertinente de la toxicité qui était prédictive d'une toxicité sous-létale à plus long terme.

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Currently accepted methods for assessing sublethal toxicity to fish are the embryo–larval or partial life cycle exposure and full life cycle (including reproduction) toxicity tests (Buikema et al. 1982). Embryo–larval tests monitor growth, development, and survival of fish from the embryo through part of the juvenile stage and have proven to be useful predictors of chronic toxicity (Macek and Sleight 1977; McKim 1977). However, embryo–larval tests require about 30 d for fathead minnows (*Pimephales promelas*), and even longer for salmonids. A reduction in exposure time, possibly by restricting the exposure period to a very sensitive life stage, would reduce effort and cost and expedite testing.

In recent years there has been a proliferation of rapid methods for sublethal toxicity assessment, most of which have been on the suborganismal level (Buikema et al. 1982). However, most physiological, biochemical, and histological measurements of toxicity have not proven to be useful due to the lack of a direct relationship between these measurements and adverse whole organism and population effects (Sprague 1976; Mehrle and Mayer 1980). Also, it is difficult to determine if a suborganismal response to a toxicant is deleterious or in the normal range of adaptation of the organism (Mount and Stephan 1967).

Growth has often been used to assess the effect of toxicants on fish (Buikema et al. 1982). However, biochemical changes during toxicosis should precede reductions in growth because growth is the culmination of many biochemical processes, and physiological and biochemical effects are the underlying cause of measurable whole organism effects (Mehrle and Mayer 1980). Toxicant effect on growth may be studied by examining macromolecules involved in growth, such as RNA, DNA, and protein. However, toxicant-induced changes in macromolecular content (RNA, DNA, and protein) and RNA/DNA, RNA/protein, and protein/DNA ratios have received very little study in fish. Kearns and Atchison (1979) correlated RNA/DNA of young-of-the year yellow perch (*Perca flavescens*) to growth rate and cadmium concentration in a metal-contaminated lake. Mudge et al. (1977) found reduced cell size and decreased cytoplasmic RNA content in the interrenal tissue of brook trout (*Salvelinus fontinalis*) acutely exposed to acid stress (pH 4.0). Stroganov (1977) found that a 24-d exposure to zinc (10 mg/L and greater) reduced the concentration of RNA in the liver and intestines of common carp (*Cyprinus carpio*) without affecting the DNA tissue concentration. Cadmium, up to lethal concentrations, did not affect RNA or DNA tissue content.

The purpose of this study was to examine the effect of short-term sublethal toxicant exposure on growth, survival, and macromolecular content of larval fathead minnows. The larval stage was used because newly hatched larvae have often been found to be the most sensitive life stage to toxicant stress (Christensen 1975; Rosenthal and Alderdice 1976; Macek and Sleight 1977; McKim 1977). Larval fathead minnows were exposed for 96 h to five chemicals to evaluate whether short-term sublethal toxicity could be detected and used to predict the effect of a toxicant on growth over a longer exposure period. The macromolecular content of larvae was studied to detect possible toxicant-induced changes prior to or concomitant with growth reduction and to gain insight into how macromolecular synthesis and cellular growth are affected by toxicant stress.

Materials and Methods

Test Conditions

Sublethal toxicity tests were conducted with fathead minnows in flow through proportional diluters (Mount and Brungs 1967) with five toxicants; hexavalent chromium (Cr), hydrogen cyanide (HCN), ethyl acetate (EA), *p*-cresol (PC), and benzophenone (BZ). For 96-h tests, fathead minnow eggs were obtained from laboratory stock and hatched in control water. Equal numbers of larval fish, within 24 h of hatching, were randomly assigned to test chambers (25–35 per chamber) and exposed for 96 h. The Cr 96-h toxicity test was conducted in hard water (see Smith et al. 1979 for water analysis) concomitant with a 28-d early life stage exposure, beginning with 1-d-old larvae. The HCN 96-h exposure was conducted in hard water as two separate tests (I and II) concomitant with a 30-d early life stage exposure. The EA, BZ, and PC 96-h toxicity tests were conducted in soft Lake Superior water at the Environmental Protection Agency Research Laboratory, Duluth, MN, concomitant with a 32-d embryo–larval exposure (beginning with the egg stage) (S. H. Poirier and L. T. Brooke, Center for Lake Superior Environmental Studies (CLSES), Superior, WI, personal communication; T. J. Norberg and D. I. Mount, Environmental Protection Agency, Duluth, MN, personal communication). Fish were fed newly hatched brine shrimp ad libitum twice per day so that moderate food accumulation occurred. In the HCN and Cr toxicity tests, diets were supplemented after day 20 with a powdered trout pellet. Fluorescent lights provided 16 h of light each day.

Water Chemistry

In the Cr and HCN toxicity tests, the experimental glass chambers measured 15 × 30 × 15 cm high and contained 5 L of test solution. Water flowed through each chamber at the rate of 200 mL/min. Water temperature was measured daily and was continuously monitored with a recording thermograph. Mean test water temperature was 25 ± 0.2°C (± SD). Toxicant stock solutions were prepared with reagent grade sodium dichromate or sodium cyanide and deionized water. Sodium hydroxide was added to obtain a HCN stock solution pH of 11.0 (Smith et al. 1979).

During Cr toxicity tests, pH was measured once per week in the control and highest treatment tanks. Mean water pH was 8.17 ± 0.06. Cr concentrations were measured twice per week by the diphenylcarbazide method (American Public Health Association 1971). During the HCN toxicity tests, pH was measured weekly in all treatment levels. Mean test water pH was 8.06 ± 0.12. HCN concentrations were measured twice per week by the colormetric method (pyridine–barbaturic acid reagent) (American Public Health Association 1975). HCN was computed from total cyanide, pH, and temperature (Smith et al. 1979). Individual treatment pH was used in calculating HCN concentrations. Test concentrations reported were derived from mean toxicant concentration over the duration of each test. Dissolved oxygen (DO) concentrations were measured daily in one control tank using the azide modification of the Winkler method (American Public Health Association 1971). In all chambers, DO was measured once per week with an oxygen meter. All tank DO were maintained at 6.1 mg/L or above by head tank aeration. Mean control chamber DO was 6.53 ± 0.22 mg/L in the Cr test and 6.83 ± 0.25 mg/L in the HCN test. Treatment chamber DO was equal to or higher than control tanks due to aeration in the toxicant mixing chamber.

Water chemistry data for the EA, BZ, and PC toxicity tests were recorded at the Environmental Research Laboratory, Duluth, MN, and can be obtained from S. H. Poirier and L. T. Brooke (EA, BZ) and T. J. Norberg and D. I. Mount (PC).

Growth Measurement

Larvae were decanted from test chambers and then pipetted onto an ice-cold glass plate to immobilize fish. No attempts to clear the gut were made (Dagg and Littlepage 1972). Eight to 15 larvae per treatment were placed in an aluminum packet and then immediately frozen in liquid nitrogen. Tissue samples were stored at −80°C until analysis to prevent enzymatic degradation of nucleic acids (Munro and Fleck 1966).

Effect of a toxicant on larval growth after 96 h of exposure was determined by measurement of length or weight. Prior to freezing, larvae from the PC and BZ 96-h toxicity tests were placed in a petri dish with a thin layer of cold water and photographed. Fish lengths were measured from the film negatives. Lengths of Cr-exposed larvae were measured on larvae from an additional 96-h toxicity test. The weight of larvae in the EA 96-h toxicity test was determined from a subsample of larvae from each treatment. Larvae were preserved in 10% formalin, dried (50°C), and then weighed to the nearest microgram on a Cahn 25 electrobalance. Neither length nor weight of larvae was measured in the HCN 96-h toxicity test.

Tissue Analysis

Frozen larvae were analyzed for RNA and DNA using a modification of the Schmidt–Thannhauser method (Munro and Fleck 1966). Larvae were homogenized with a Wheaton teflon motor-driven tissue grinder in ice-cold 0.2 mol percloric acid (PCA)/L. Interfering acid-soluble, low molecular weight compounds (e.g. nucleotides, amino acids) were removed in the supernatant after centrifugation. Homogenized samples were analyzed immediately to prevent degradation of nucleic acids (Hutchison et al. 1962). All centrifugations were carried out at 10 000 × *g* for 10 min at 2–4°C. Supernatants were aspirated rather than decanted to prevent sediment loss. Lipid extraction was deemed unnecessary because of lack of interference by these compounds (Fleck and Munro 1962). RNA was hydrolyzed in 0.3 mol KOH/L at 37°C for 60 min (Buckley 1979). RNA was quantified by UV absorbance of the supernatant at 260 nm on a Beckman DBGT spectrophotometer using calf thymus RNA (Sigma Chemical Co.) as a standard. DNA was hydrolyzed by heating in 0.6 mol PCA/L at 82–84°C for 15 min. The hydrolyzed DNA supernatant was quantified by UV absorbance at 268 nm (maximum absorbance of PCA-hydrolyzed DNA) (Swift 1955) using salmon testes or calf thymus DNA as a standard. Nucleic acid supernatants were centrifuged to remove suspended particles before reading spectrophotometrically. Standards were treated the same as the samples and calibration curves were linear over the range of the samples.

After nucleic acid extraction, the remaining pellet was washed, dried at 40–50°C, and stored frozen at −20°C until protein analysis. For protein analysis, the pellet was initially hydrolyzed in 1 mol NaOH/L at 95°C for 1 h. A 100-μL subsample was analyzed colorometrically by Hartree's (1972) modification of the Lowry method, using bovine serum albumen (BSA) as a standard (Lowry et al. 1951). Data were expressed as average quantity of RNA, DNA, or protein per whole larva, ratios of macromolecular content, or tissue concentration.

Analytical Variability

The extraction efficiency of the complete analytical procedure for nucleic acids and protein was checked using a mixture of known quantities of RNA, DNA, and protein. Mean percentage recovery (± SE) was 81.2 ± 1.4, 73.0 ± 6.9, and 100.6 ± 1.8 for RNA, DNA, and protein, respectively. Small amounts of sediment loss during the initial washing would have resulted in a large loss of nucleic acids, since spiked samples were not used. Actual recovery in fish tissue would be expected to be higher and less variable because sediment loss would have much less effect with a low percentage content of nucleic acids.

The hot acid separation of DNA from protein was checked to determine if significant protein contamination of the DNA supernatant occurred due to protein solubilization during DNA extraction. This PCA hydrolysis recovered about 89% DNA with less than 1% error due to protein contamination in samples prepared with known quantities of DNA and protein (Barron 1982).

The precision of the RNA and DNA analysis was checked by simultaneously analyzing six 200-μL aliquots from a homogenate of 75 fathead minnow larvae. Coefficients of variation were 4.7, 5.0, and 0.3% for RNA, DNA, and RNA/DNA, respectively.

Statistical Analysis

Effect of a toxicant on growth and macromolecular content was examined by log-linear dose–response analysis (Casarett 1975). Individual toxicity tests were analyzed as randomized block designs with two or four replicates as blocks (Cochran and Cox 1957): Cr (control and six treatments, four replicates), HCN I and II (control and six treatments, two replicates), EA, PC, and BZ (control and five treatments, two replicates). Test chambers were considered the experimental units and mean tank response was used in the analysis (McClave et al. 1981). The presence of significant treatment effects was determined by two-way analysis of variance (ANOVA, $\alpha = 0.05$). Block sum of squares and degrees of freedom were combined with the error term when blocking was not significant. Missing data were estimated for 96-h macromolecular content in one replicate of the Cr (1.15 mg/L) and HCN I (107.06 μg/L) toxicity tests. A modified ANOVA was used with the loss of one degree of freedom for each estimated missing datum (Weisberg and Koehler 1979). The lowest toxicant concentration causing a significant treatment effect was determined by Dunnets multiple range test, one-sided at $\alpha = 0.05$ (Steel and Torrie 1960). Regression analysis was performed by least squares regression (Neter and Wasserman 1974).

Results

Hexavalent Chromium

The most sensitive response measured in the Cr 28-d early life stage test (larval through juvenile stage) was growth, which was reduced ($P < 0.05$) at 1.86 mg Cr/L (Fig. 1A). Ninety-six-hour larval growth (in length) was reduced at 6.62 mg Cr/L ($P < 0.05$), while no effect on survival at 96 h occurred at any concentration tested (Fig. 1A). Larval macromolecular content (RNA, DNA, and protein) after 96 h of exposure was reduced at 5.13 mg Cr/L ($P < 0.05$) (Fig. 1B). RNA content per larva was the measurement most responsive to Cr exposure, with a 63% reduction from the control level at the highest concentration tested (Fig. 1B). RNA/DNA and RNA/protein ratios were reduced at 5.13 mg Cr/L ($P < 0.05$), but no significant effect on protein/DNA was found at any concentration tested (Fig. 1C). RNA and DNA content and RNA/protein exhibited subinhibitory response stimulation (hormesis), as did 28-d growth.

Hydrogen Cyanide

The most sensitive response measured in the HCN 30-d early life stage test was growth, which was reduced ($P < 0.05$) at 47.15 μg HCN/L (Fig. 2A). Ninety-six-hour exposure was conducted in two separate tests (HCN I and HCN II) (Barron 1982). Survival to 96 h was reduced ($P < 0.05$) in the highest treatment, as this concentration (107.06 μg HCN/L) was near the 96-h median lethal concentration for larval fathead minnows (Fig. 2A) (Smith et al. 1979). Growth at 96 h was not measured. Reductions ($P < 0.05$) in RNA content per larva occurred at 35.54 μg HCN/L and in DNA and protein at 57.99 μg HCN/L in test I, while reduction in RNA, DNA, and protein content occurred at18.54 μg/L in test II (Fig. 2B). The lower HCN concentration causing a significant effect in test II was partly due to lower variability of the responses (lower mean square error). No effect on RNA/DNA, RNA/protein, or protein/DNA was found at any HCN concentration tested (Fig. 2C).

Ethyl Acetate

The most sensitive response measured in the EA 32-d embryo–larval test (embryo through juvenile stage) was growth, which was reduced ($P < 0.05$) at the lowest EA concentration tested (9.65 mg/L) (Fig. 3A) (S. H. Poirier and L. T. Brooke, personal communication). However, the relationship between growth and toxicant concentration in the EA embryo–larval test was not linear; the greatest reduction in growth (47%) occurred at the lowest EA concentration (Fig. 3A). Ninety-six-hour larval growth (in weight) was reduced ($P < 0.05$) at 19.40 mg EA/L, while no effect on survival to 96 h occurred (Fig. 3A). Larval macromolecular content was significantly reduced ($P < 0.05$) at 19.40 mg EA/L, although reductions occurred at the lowest EA concentration tested (Fig. 3B). RNA content per larva was the most responsive measurement of toxicant stress at all EA concentrations. RNA/DNA and RNA/protein were also reduced ($P < 0.05$) at 19.40 mg EA/L, while protein/DNA was only reduced at 75.6 mg/L (Fig. 3C).

Percentage dry weight of RNA, DNA, and protein in the EA 96-h toxicity test was analyzed to determine if toxicant effect on the concentration of macromolecules in larval tissue was more

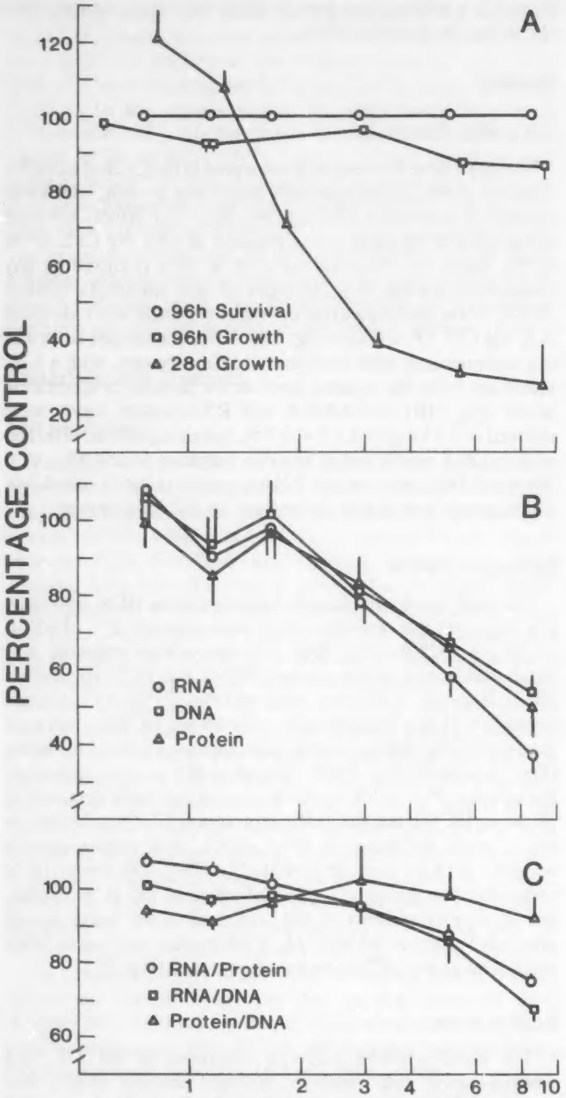

FIG. 1. Dose-response curves for hexavalent Cr. Data are normalized as percentage of the mean control level. Actual numbers can be derived from the control levels. Control levels: (A) 96-h survival, 100%; 96-h growth, 7.6 mm; 28-d growth, 99.93 mg; (B) RNA, 34.25 μg/larva; DNA, 11.21 μg/larva; protein, 259.30 μg/larva; (C) RNA/protein, 131.50 μg/mg; RNA/DNA, 3.05 μg/μg; protein/DNA, 23.26 μg/μg. Absent standard error bars are contained within the symbol for the mean.

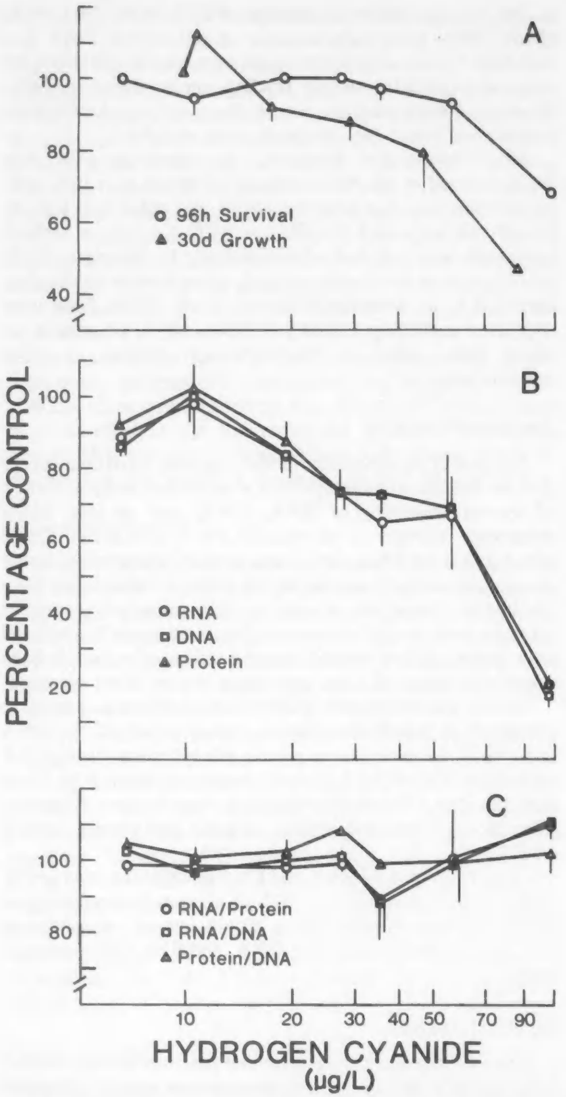

FIG. 2. Dose–response curves for HCN. Results from HCN I and HCN II 96-h exposures (as percentage of control level) at HCN concentrations within 10% of each other were combined and expressed as a mean percentage at that mean concentration. Data are normalized as percentage of the mean control level. Actual numbers can be derived from the control levels. Control levels: (A) 96-h survival, 100%; 30-d growth, 181.7 mg; (B) RNA, 12.76 μg/larva; DNA, 5.44 μg/larva; protein, 150.41 μg/larva; (C) RNA/protein, 84.29 g/mg; RNA/DNA, 2.33 μg/μg; protein/DNA, 28.08 μg/μg. Absent standard error bars are contained within the symbol for the mean.

sensitive than effects reported for whole larval content. A subsample of 10 fish per chamber for weight determination made this analysis possible (Table 1). Ethyl acetate exposure (49.40 mg/L) resulted in significant reduction only in the tissue concentration of RNA. Protein tissue concentration was reduced only 4%, while DNA tissue concentration was increased 6% relative to the control level at the EA concentration causing significant reduction in whole larval content. These data are in agreement with results for whole larvae (Fig. 3B), although tissue concentration was less sensitive to toxicant stress than whole larval nucleic acid and protein content.

p-Cresol

The most sensitive response measured in the PC 32-d

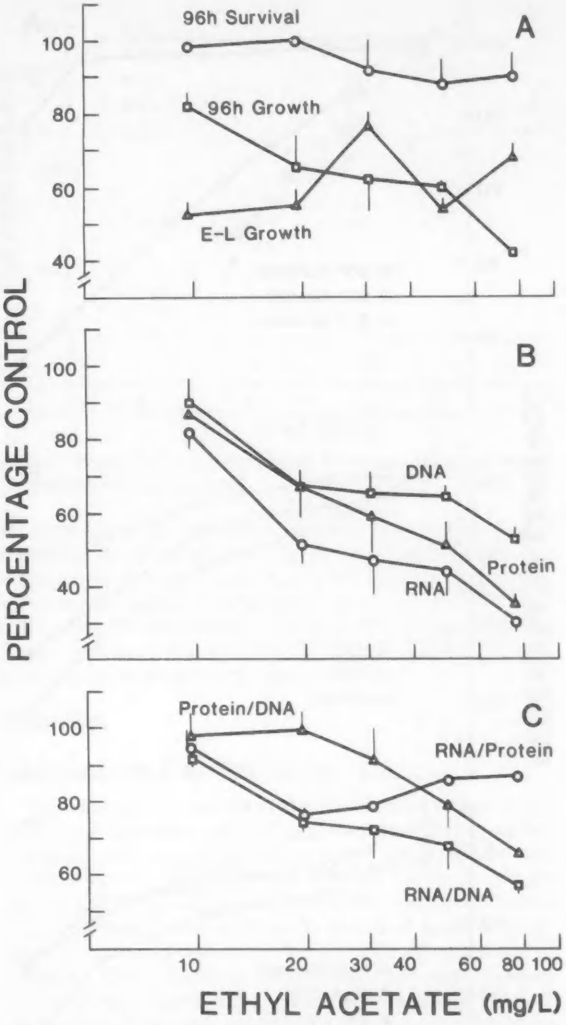

FIG. 3. Dose–response curves for EA. Data are normalized as percentage of the mean control level. Actual numbers can be derived from the control levels. Control levels: (A) 96-h survival, 100%; 96-h growth, 251.6 μg; embryo–larval (E–L) growth, 117.0 mg; (B) RNA, 13.58 μg/larva; DNA, 5.95 μg/larva; protein, 138.30 μg/larva; (B) RNA/protein, 98.16 μg/mg; RNA/DNA, 2.28 μg/μg; protein/DNA, 23.24 μg/μg. Absent standard error bars are contained within the symbol for the mean.

TABLE 1. Effect of EA 96-h exposure on the tissue concentration of RNA, DNA, and protein of larval fathead minnows. Data are presented as percentage dry weight (μg/μg tissue × 100). Standard errors are given in parenthesis. Significant treatment effects: *$P < 0.05$, **$P < 0.01$.

EA (mg/L)	Dry weight (μg)	RNA (%)	DNA (%)	Protein (%)
0	251.55 (6.45)	5.40 (0.24)	2.37 (0.05)	55.01 (1.21)
9.65	205.55 (9.74)	5.46 (0.56)	2.62 (0.31)	58.73 (3.04)
19.40	164.37* (22.63)	4.21 (0.16)	2.45 (0.17)	56.10 (0.85)
30.08	155.52** (21.59)	4.06 (0.25)	2.50 (0.11)	52.33 (2.64)
49.40	150.17** (4.33)	3.99* (0.45)	2.55 (0.05)	46.95 (4.68)
75.60	105.37** (2.96)	3.88* (0.25)	2.95 (0.12)	45.37 (2.26)

embryo–larval exposure was growth, which was reduced ($P < 0.05$) at 2.57 PC/L (T. J. Norberg and D. I. Mount, personal communication) (Fig. 4A). No significant effect on larval survival or growth occurred during the PC 96-h toxicity test (Fig. 4A). Larval macromolecular content, although reduced at 2.57 mg PC/L, was not significantly affected at any PC concentration tested (Fig. 4B). RNA content per larva was the 96-h measurement most responsive to toxicant stress (43% maximum reduction). The RNA/DNA ratio was reduced ($P < 0.05$) from the control level, while no significant effects on protein/DNA or RNA/protein occurred (Fig. 4C). Significant treatment effects for RNA/DNA occurred at 0.40 and 4.20 mg PC/L. The relatively low RNA/DNA at 0.40 mg PC/L was apparently anomalous, since a log-linear dose–response relationship was present only for PC concentrations greater than 0.40 mg/L (Fig. 4). Also, trends in macromolecular content were the opposite of RNA/DNA, RNA/protein, and protein/DNA only at this concentration. The drastic reduction at 0.40 mg/L was caused by a 30% increase in DNA, while RNA levels remained similar to the control. Hormetic stimulation occurred in both embryo–larval growth and macromolecular content.

Benzophenone

The most sensitive response measured in the BZ 32-d embryo–larval test was growth in weight, which was reduced ($P < 0.05$) at the lowest BZ concentration (0.99 mg/L) (S. H. Poirier and L. T. Brooke, personal communication) (Fig. 5A). Growth in length was only reduced ($P < 0.05$) at 1.78 mg BZ/L. Growth of BZ 96-h exposed larvae was reduced ($P < 0.05$) at 2.62 mg/L, although growth was relatively unresponsive to toxicant exposure (as percentage reduction) (Fig. 5A). Survival to 96 h was only reduced at the highest BZ concentration. Larval RNA and protein content were reduced ($P < 0.05$) at 5.15 mg BZ/L, while DNA content was reduced at 8.28 mg/L (Fig. 5b). RNA content was the 96-h measurement most responsive to BZ exposure. RNA/DNA and protein/DNA were reduced at 5.15 mg BZ/L and RNA/protein was reduced at 8.28 mg/L ($P < 0.05$) (Fig. 5C).

Relationships Between RNA, DNA, and Protein

Various indicators of current growth rate or achieved growth were compared for their consistency. The RNA/DNA ratio of fathead minnow larvae was very sensitive to toxicant exposure and was highly correlated with larval protein content after 96 h of exposure to Cr, EA, PC, and BZ (Fig. 6). Larval proetin content after 96 h should have been analogous to protein growth rate because larvae were initially exposed at the same size and age. RNA/DNA explained 67.9% of the variation in protein content for all toxicants combined and 90.2% with PC omitted. Protein and DNA were highly correlated ($r = 0.943$) for all toxicants combined, showing the consistency of these two measures of growth (Fig. 7). RNA and protein generally decreased concomitantly with toxicant concentration, but with

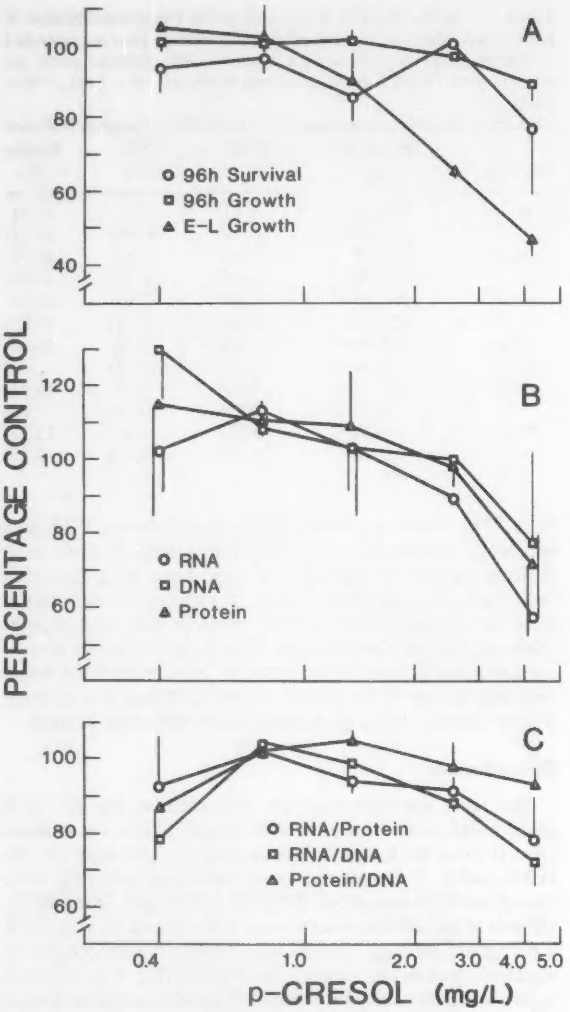

FIG. 4. Dose–response curves for PC. Data are normalized as percentage of the mean control level. Control levels: (A) 96h survival, 100%; 96-h growth, 7.40 mm; E–L growth, 232.0 mg; (B) RNA, 16.79 μg/larva; DNA, 4.58 μg/larva; protein, 143.80 μg/larva; (C) RNA/protein, 116.58 μg/mg; RNA/DNA, 3.69 μg/μg; protein/DNA, 31.65 μg/μg. Absent standard error bars are contained within the symbol for the mean.

RNA generally decreasing at a faster rate (i.e. reduced RNA/protein).

Correlation and Prediction of Long-Term Growth

The similarity of dose–response relationships for longer term exposure (28–32 d) and 96-h exposure was evaluated by regression analysis of early life stage growth on 96-h growth or macromolecular content (Table 2). Growth and macromolecular content (96 h) in the Cr, HCN, PC, and BZ toxicity tests were highly correlated with early life stage growth, indicating that the dose–response relationships for 96-h and longer term exposure were similar. The EA embryo–larval growth data were less highly correlated ($r < 0.50$) with 96-h measurements due to the lack of a linear dose–response relationship for growth (Fig. 3A).

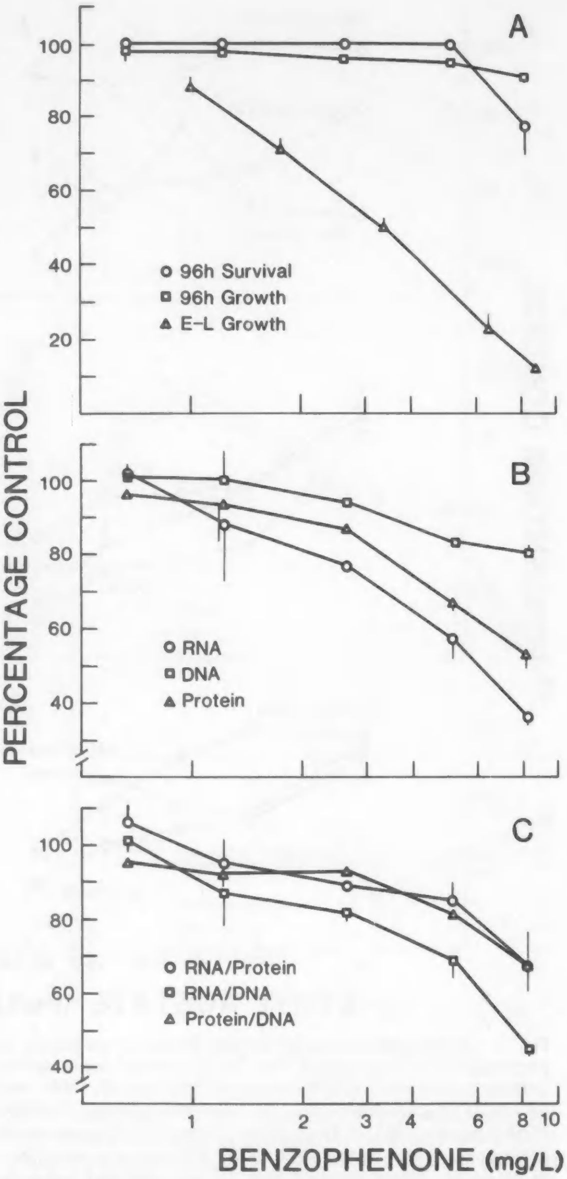

FIG. 5. Dose–response curves for BZ. Data are normalized as percentage of the mean control level. Control levels: (A) 96-h survival, 100%; 96-h growth, 5.95 mm; E–L growth, 155.36 mg; (B) RNA, 5.66 μg/larva; DNA, 3.47 μg/larva; protein 72.72 μg/larva; (C) RNA/protein, 77.44 μg/mg; RNA/DNA, 1.62 μg/μg; protein/DNA, 20.88 μg/μg. Absent standard error bars are contained within the symbol for the mean.

The range of "safe" concentrations estimated from 96-h macromolecular content, ratios, or growth fell within or very near the range of "safe" levels determined by full life cycle or early life stage exposure, and interestingly, HCN 96-h "safe" levels were more similar to full life cycle data than those from

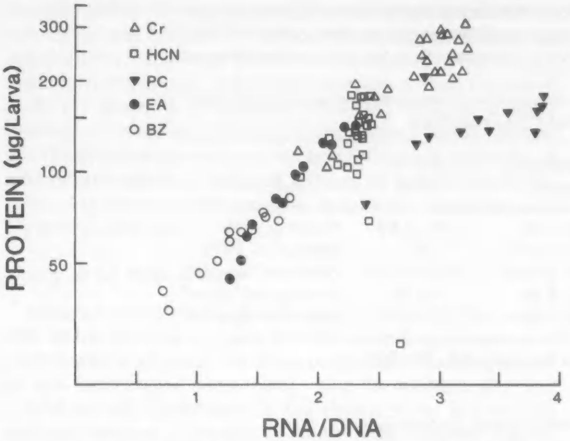

FIG. 6. Regression plot of larval RNA/DNA ratio on protein content after 96 h of toxicant exposure.

the early life stage exposure (Table 3). The range of "safe" concentrations are defined as the toxicant concentrations between the highest test concentration not causing a significant effect and the lowest concentration causing a significant ($P < 0.05$) treatment effect. Thus, 96-h growth and macromolecular content appeared to be relatively accurate predictors of effects occurring in the longer term exposures.

Discussion

Relationship with Long-Term Growth

Significant whole organism toxicosis occurred within 96 h of early larval exposure, and the toxicant concentration causing that stress was very similar to that which caused longer term sublethal effects. The regression analyses (Table 2) and the similarity of predicted "safe" levels (Table 3) suggest that 96-h toxicant exposure, during the early period of larval development, at least partly determined fish size after a longer period of exposure. The similarity of 96-h and early life stage exposure dose–response relationships implied similar causal relationships, although the similarity of slopes was not tested due to the curvilinear function of the dose–response curves. In general, RNA content per larva was the measurement most highly correlated with early life stage growth. Several toxicant concentrations substantially reduced macromolecular content of larvae even though the values were not statistically different from the control level. Additional replicates and a larger sample size (per concentration) should provide increased statistical sensitivity for the methodology and thus should yield results even more similar to longer term exposures.

Toxicant Effect on Cellular Growth

Sublethal toxicant exposure of larvae to Cr, HCN, EA, and BZ resulted in a significant reduction in DNA content after 96 h of exposure, and in all toxicity tests larval DNA content responded to toxicant concentration in a dose-dependent manner. A lower DNA content indicated that toxicant-exposed fish had fewer cells and thus had experienced reduced growth rates, probably due to mitotic suppression (Hotchkiss 1955; Winick and Noble 1965; 1966). The lack of elevation of protein/DNA ratios after 96 h of toxicant exposure indicated an absence of toxicant-induced hypertrophy (Winick and Noble 1965, 1966; Goss 1966).

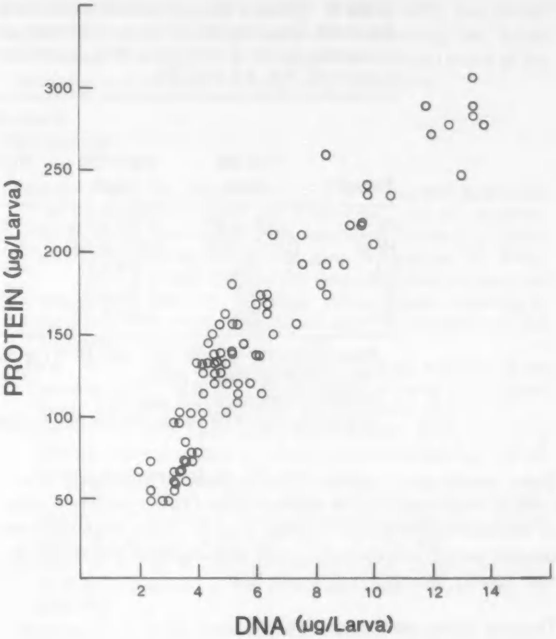

FIG. 7. Regression plot of DNA on protein (µg/larva) after 96-h exposure for all toxicants combined.

TABLE 2. Correlations (r) between early life stage growth (28–30 d) and 96-h RNA, DNA, and protein content, RNA/DNA, and growth (length or weight) paired at each toxicant concentration. NA, not available.

96-h measurement	Toxicant				
	Cr[a]	HCN[a,b]	EA	PC	BZ[a]
RNA	0.891	0.976	0.416	0.951	0.990
DNA	0.899	0.994	0.378	0.810	0.974
Protein	0.823	0.990	0.352	0.917	0.976
RNA/DNA	0.773	(−)0.687	0.364	0.625	0.971
Growth	0.701	NA	0.429	0.957	0.947

[a] Early life stage growth estimated by log-linear interpolation at the 96-h concentration due to mean treatment concentrations being slightly different (see corresponding figures).

[b] Data from HCN I (Barron 1982).

Protein/DNA (cell mass) was generally insensitive to toxicant exposure, with significant reductions only in the EA and BZ toxicity tests. Protein/DNA ratio was significantly reduced in the EA toxicity test only at a concentration three times the dosage that caused significant reductions in macromolecular content and RNA/DNA and RNA/protein ratios. Protein/DNA ratio in the BZ 96-h test was responsive to toxicant exposure, which may have been related to the mechanism of BZ sublethal toxicity. Since larval DNA content was generally more sensitive than protein/DNA ratio to toxicant exposure, toxicant effect on larval growth and development appeared to occur primarily by reducing the rate of cell multiplication (mitosis) rather than by restricting cell enlargement (see Winick and Noble 1965).

TABLE 3. Range of toxicant concentrations (mg/L) between the highest tested concentration causing no significant effect and the lowest concentration causing a significant treatment effect (range of "safe" concentrations) for five toxicants. Data for macromolecular content are from the most sensitive response in each test. NA, not available.

	Range of "safe" concentrations				
Toxicant	Full life cycle	Early life stage	Macromolecular content	Growth (96 h)	Reference[a]
Cr	1.00–3.95	1.25–1.86	2.98–5.13	3.00–5.59	Pickering 1980
HCN	0.013–.020	0.029–0.047	0.010–0.019[b]	NA	Smith et al. 1979
EA	NA	<9.65	9.65–19.40	9.65–19.40	Poirier and Brooke[c]
PC	NA	1.35–2.57	2.57–4.20	>4.20	Norberg and Mount[c]
BZ	NA	1.00–1.78[d]	2.61–5.15	1.22–2.61	Poirier and Brooke[c]

[a] Data source for full life cycle (Cr, HCN) or partial life cycle (EA, PC, BZ).

[b] From HCN II (Barron 1982).

[c] Personal communication (see text).

[d] Significant effect on weight but not length at the lowest tested concentration.

These results are in agreement with those of Weatherly et al. (1980), who found that in rainbow trout (*Salmo gairdneri*) (up to 20 cm),recruitment of mosaic muscle fibers responded to somatic growth rate changes, while fiber diameter was similar in very rapidly and slowly growing fish.

Toxicant Effect on Protein Synthesis

Sublethal toxicant exposure of larvae to Cr, HCN, EA, and BZ resulted in significant reduction in RNA and protein content after 96 h of exposure. In all 96-h toxicity tests, RNA and protein content per larva was reduced from the control level and responded to toxicant concentration in a dose-dependent manner. RNA content per larva was the most responsive measurement (as percentage reduction) in 96-h toxicity tests for all chemicals studied. A reduction of RNA content per larva (relative to the control level), with concomitant protein and DNA reductions, indicated that toxicant-stressed larvae had a reduced net rate of protein synthesis, probably mediated through declines in RNA (Buckley 1980; Love 1980). Toxicant-stressed larvae had lower RNA content than control fish for two apparent reasons: toxicant-stressed larvae (1) were smaller (i.e. fewer cells) and (2) generally had lower RNA/DNA ratios (i.e. less RNA per cell).

The RNA/DNA ratio of larval fathead minnows was significantly reduced at concentrations similar to those causing reduced growth during longer term exposures to Cr, EA, PC, or BZ. However, HCN exposure resulted in decreased larval RNA, DNA, and protein content, while RNA/DNA was highest at the highest HCN concentration. This may have been due to the rapid toxic action of HCN early in the 96-h exposure period. Leduc (1977) also has reported an acceleration of growth following an initial depression in several species of fish exposed to sublethal levels of HCN. RNA/DNA appears to be sensitive to environmental variables and to the physiological state of the fish (Haines 1973, 1980). The results of the present study demonstrate that RNA/DNA ratio is also sensitive to sublethal toxicant exposure.

RNA/DNA appeared to be a sensitive index of protein growth rate in both control and toxicant-stressed fish (Fig. 6). Buckley (1979, 1980) also found that RNA/DNA was highly correlated with growth rate (in weight) and protein growth rate of winter flounder (*Pseudopleuronectes americanus*) and Atlantic cod (*Gadus morhua*) larvae. The most rapidly growing larval fathead minnows (as indicated by RNA/DNA, RNA, DNA, and protein content, and growth) in 96-h toxicity tests generally also had the highest RNA/protein ratios. RNA/protein ratios have been found to increase during periods of rapid growth (in two species of Crustacea) and to decrease in the offspring of methodone-dosed rats (Dagg and Littlepage 1972; Peters 1977).

Toxicant Effect on Macromolecular Content

All toxicants elicited reduced nucleic acid and protein content at high concentrations and had a threshold level of toxicity. Toxicant exposure to sublethal concentrations of Cr and PC resulted in hormetic stimulation in early life stage growth and 96-h macromolecular content. Toxicant-induced stimulation of nucleic acid and protein content indicated an acceleration of cellular metabolism and growth (Steel and Johannesson 1975; Peters 1977; Love 1980) that may have been responsible for the observed stimulation of juvenile growth. In larval fathead minnows, toxicant exposure appears to slow elaboration of nucleic acids and protein during the 96-h exposure period, rather than cause a net loss from initial levels (M. G. Barron and I. R. Adelman, unpublished data). Toxicant effect on macromolecular content is often due to an indirect action on nucleic acid and protein synthesis, since a toxicant that interferes with energy-yielding reactions is indirectly an inhibitor of the syntheses of RNA, DNA, and protein (Holbrook 1980). A toxicant is probably acting in such a manner if the chemical inhibits the synthesis of all three macromolecules by comparable levels in dose–response experiments (Holbrook 1980). The results presented here for five chemicals suggest that toxicant action appeared to be an indirect effect on macromolecular synthesis, since RNA, DNA, and protein content had comparable dose-dependent reductions in all 96-h toxicity tests.

Toxicant effect may have been due to an inhibition of energy-yielding processes, channeling of energy for maintenance of homeostasis, or interference with appetitive behavior. Although chemical exposure can affect feeding behavior (Drummond et al. 1973), it is unlikely that an inhibition of appetitive behavior would be a direct effect from the chemicals used in this study, but rather a secondary effect induced by physiological stress. The known modes of toxic action of HCN (oxidative phosphorylation inhibition), Cr (direct binding with nucleic acids and proteins), BZ (narcosis), and PC (CNS depression) support a mechanistic effect on macromolecular content, rather than a direct effect on appetitive behavior (Goodman and Gilman 1975; U.S. Environmental Protection Agency 1980; Veith et al. 1983). The mechanism of EA toxicity is not currently known. A plausible toxicosis scenario appeared to be (1) initiation of toxicant stress (via toxicant–receptor binding), (2) metabolic energy diverted from anabolic processes, direct interaction with nucleic acid and protein synthesis, or inhibition of appetitive behavior, (3) decline in net cellular RNA levels, (4) slowed protein synthesis and mitotic supression, and (5) growth reduction.

Utility of the Methodology

Measurement of larval growth and macromolecular content after 96 h of toxicant exposure provides several useful indices of sublethal toxicity. Selection of one particular 96-h measurement to use entails two components: ease of measurement and reliability and consistency of the measurement in assessing sublethal toxicity. Changes in tissue mass (growth) can be assessed by a relatively simple measurement of tissue weight or protein content. Weight, however, is a very nonspecific measurement, since it reflects not only changes in protein content but also the degree of tissue hydration, lipid content, and glycogen storage (Love 1970). Macromolecular content, and ratio, were sensitive to toxicant exposure and also provided some insight into how growth of the larvae was affected. However, it is best to use all of the indices presented here, since no single index consistently yielded the lowest "safe" concentration.

It has been extensively reported in the literature that embryo–larval exposure results in significant deleterious effects at levels similar to those in full life cycle exposures (including reproduction) (see reviews by Macek and Sleight 1977 and McKim 1977). However, the 32-d embryo–larval exposure period for fathead minnows (a common test species) appears to have been arbitrarily selected, with few attempts to investigate if a reduction in exposure time would affect results. The 96-h methodology proposed here omits juvenile and embryo exposure and thus contributes no knowledge of the toxicity to the embryo or teratology of the chemical. However, the procedure appears to be useful as an estimator of chronic toxicity. The 96-h methodology should be useful as a rapid screening method for the sublethal toxicity of chemicals to fish, particularly for those species not generally amenable to laboratory toxicity testing. The methodology may also be very useful as a range-finding tool for locating concentrations to be used in longer term tests. The utility of the methodology is obviously limited by the growth rate of control fish, since toxicant effect is judged by the difference between control and treatment groups. However, a toxicant initiating a physiological stress that induces adjustments in homeostatic processes of an organism should impose changes in nucleic acid or protein content indicative of changes in cellular metabolism.

Acknowledgments

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Susceptibility of Grey (*Halichoerus grypus*) and Harp (*Phoca groenlandica*) Seals to the Influenza Virus and Mycoplasma of Epizootic Pneumonia of Harbor Seals (*Phoca vitulina*)

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Six grey, *Halichoerus grypus*, and 12 harp, *Phoca groenlandica*, seals were inoculated intratracheally with lung homogenate containing influenza virus A/seal/Mass/1/80 and mycoplasma from harbor seals, *Phoca vitulina*, which had died in an epizootic of pneumonia. The grey seals were refractory to infection, whereas some of the harp seals developed mild pneumonia. Virus was recovered from 4 of 10 harp seals necropsied, and antibodies were produced in 2 survivors. The mycoplasma given alone to 2 grey seals did not replicate or produce infection and was recovered from only 1 of 12 harp seals inoculated. We examined 99 grey, 102 harp, 14 harbor, and 7 hooded seals (*Cystophora cristata*) from eastern Canada and found antibodies to avian influenza A/seal/Mass/1/80 in 3 adult male grey seals from Sable Island, N.S.; this virus is apparently adaptable to other seal species. Related forms of the virus are highly suspect as the cause of past epizootics, and one is currently responsible for a new outbreak of pneumonia in New England harbor seals.

On a inoculé dans la trachée à 6 phoques gris (*Halichoerus grypus*) et à 12 phoques du Groenland (*Phoca groenlaudica*) un broyat de poumon contenant le virus de la grippe A/seal/Mass/1/80 et du mycoplasme provenant de phoques communs (*Phoca vitulina*), qui sont morts lors d'une épizootie de pneumonie. Les phoques gris étaient réfractaires à l'infection, tandis que certains des phoques du Groenland ont développé une pneumonie bénigne. Le virus a été récupéré de 4 des 10 phoques du Groenland autopsiés, et des anticorps ont été produits chez 2 survivants. Le mycoplasme administré seul à 2 phoques gris n'a pas fait réapparaître ou produit d'infection et a été récupéré d'un seul des 12 phoques du Groenland inoculés. Nous avons examiné 99 phoques gris, 102 phoques du Groenland, 14 phoques communs et 7 phoques à capuchon (*Cystophora cristata*) venant de l'est du Canada et nous avons trouvé des anticorps à la grippe aviaire A/seal/Mass/1/80 chez 3 phoques gris mâles adultes provenant de l'île-de-Sable (N.-É.) ; ce virus peut apparemment s'adapter à d'autres espèces de phoques. Des formes apparentées du virus sont grandement suspectes comme la cause d'épizooties passées, et une d'entre elles est actuellement responsable d'une nouvelle recrudescende de pneumonie chez les phoques communs de la Nouvelle-Angleterre.

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During a 10-mo period beginning December 1979, an epizootic of pneumonia killed at least 450 harbor seals, *Phoca vitulina*, along the New England coast. Affected seals were weak, uncoordinated, and breathed only with great difficulty; they died of acute hemorrhagic pneumonia. The disease seemed first to affect juvenile seals within the Cape Cod area but soon dispersed northward along the coast of Maine (Geraci et al. 1982). The cause of the disease was avian influenza virus A/seal/Mass/1/80 (H7N7) (Lang et al. 1981; Webster et al. 1981) in possible association with a new mycoplasma species (Geraci et al. 1982).

The epizootic showed remarkable similarities to undiagnosed mass mortalities in other seal species (Geraci et al. 1982). We therefore undertook laboratory experiments to determine whether the agents associated with disease in the harbor seals could cause infection in the closely related harp seal, *Phoca groenlandica*, and the grey seal, *Halichoerus grypus*, whose ranges overlap that of the harbor seals. We also conducted field surveys to establish whether the virus or antibodies to it could be detected in free-ranging seals as far north as Newfoundland.

Materials and Methods

Laboratory Studies

Experimental animals

Seals were captured from breeding and haul-out areas off the Atlantic coast of Canada. Eight 1-mo-old grey seal pups (5 females, 3 males) from Amet Island, N.S., and twelve 1-mo-old harp seal pups (10 females, 2 males) from the Magdalene Islands, Que., were transported to the University of Guelph. Two 4-mo-old female harbor seals from Sable Island, N.S., were used as controls. The grey seals were kept on snow in an outdoor fenced enclosure for up to 28 d before being brought into indoor isolation facilities for experimentation. Harp and harbor seals were placed directly in 15–18°C isolation rooms, where they were held in 1.5 × 2 m dog kennels with screen mesh flooring. The seals had access to small tubs of water. All seals were fasted during the experiment.

Virus inoculation

Six grey seals (4 females, 2 males) and 8 harp seals (7 females, 1 male) were each inoculated intratracheally with 2 mL of a homogenate prepared from the lung of a harbor seal that died of the natural disease. The homogenate contained $10^{8.0}$ EID_{50} virus/g (Webster et al. 1981) and *Mycoplasma* sp. strain No. M4359 (Ontario Ministry of Agriculture and Food, Veterinary Services Laboratory, Guelph, Ont.). Seals were inoculated while physically restrained or chemically immobilized (Geraci et al. 1981).

Blood samples and culture swabs were taken before and 0.5, 1, 1.5, 2.5, 3.5, 4.5 and 5.5 d following inoculation in the grey seals and 1, 2, 3, 6, 7, 13, 20, and 27 d in the harp seals. Blood from the hind flippers (Geraci 1971) was collected into EDTA-treated Vacutainer tubes (Becton, Dickinson and Co., Canada Ltd., Mississauga, Ont.) for hematology and into untreated Vacutainer tubes for antibody titers (Webster et al. 1981). Differential white blood cell counts were made from smears stained with Wright's stain. Virus isolation (Webster et al. 1981) was attempted from rectal and conjunctival swabs and from nasal washings obtained by infusing 3–5 mL of sterile saline into each nostril of the seal. These samples were frozen at −70°C within 2 h of collection and stored for up to 1 mo. Swabs of nasal, conjunctival, and oral mucosa were cultured for mycoplasma using two media, one containing porcine serum (Ruhnke et al. 1978) and the other containing horse serum (Davies 1967).

Grey seals were killed for necropsy examination 1.5, 2, 4.5, 5 (two seals), and 5.5 d after infection. Six harp seals were killed in pairs at each of 2, 3, and 7 d after inoculation; two harp seals were retained for observation and were bled weekly for 4 wk to measure antibody titers.

Tissues taken at necropsy were fixed in 10% neutrally buffered formalin for light microscopy. For virus isolation (Webster et al. 1981), samples of lung, brain, liver, spleen, kidney, and colon, and bronchial, gastric, and mandibular nodes were frozen within 1 h of death and stored at −70°C for up to 1 mo. Lung, brain, spleen, kidney, and bronchial node samples were collected and cultured for mycoplasma, as described above.

Mycoplasma inoculation

Two grey seal pups (1 female, 1 male) were each inoculated intratracheally with 1 mL of broth suspension containing 1.9×10^9 mycoplasma M4359 originally isolated from harbor seal lung. The isolate had been subcultured twice and stored at −70°C for 12 mo. The third subculture was then suspended in broth supplemented with 20% porcine serum. After 24 h of aerobic incubation at 37°C, the culture was dispensed into ampules and stored in liquid nitrogen for 1 wk. The inoculum given the seals was in the fifth subculture and was prepared by growing the liquid nitrogen-stored mycoplasma for 24 h at 37°C in 200 mL of broth, centrifuging the medium, and resuspending the pellet in 2 mL of supernatant.

Blood samples and conjunctival and nasal swabs were obtained at 1- to 3-d intervals over a 12-d period and processed as described above. Both seals were killed 12 d after inoculation for postmortem examination and tissue sampling.

Mycoplasma and virus inoculation

Four harp seals (3 females, 1 male) were each inoculated intratracheally with 2 mL of a suspension containing 7.4×10^9 mycoplasma M4359/mL. The inoculum was prepared from the previously described culture, which had been stored in liquid nitrogen for 7 wk. After 48 h of growth at 37°C in 700 mL of broth, the culture was concentrated by centrifugation and resuspended in 10 mL of the supernatant.

Four and 5 d after inoculation with the mycoplasma culture, the harp seals were each given two doses of harbor seal lung homogenate containing influenza A virus (2 mL at $10^{6.5}$ EID_{50}/g) and mycoplasma M4359. Blood samples and culture swabs were taken daily for 6 d and on the 10th d after the first inoculation with lung homogenate. Two of the seals were killed after 5 d and two after 10 d. Samples for histopathology and microbiology were collected as previously described.

Controls

Two harbor seals were inoculated intratracheally with 2 mL of a sterilized homogenate of harp seal lung. The tissue was homogenized in phosphate-buffered saline and centrifuged at 120 × *g* for 3 min at 4°C, and 10 mL of the supernatant was placed in a petri dish and irradiated for 30 min with 14 Gy/min. Blood and nasal swabs were taken before inoculation, and 48 h after, when the seals were killed for necropsy and collection of tissues for culture.

Field Studies

Fourteen adult harbor seals (4 females, 10 males), 77 adult grey seals (39 females, 38 males), and 22 one-month-old grey seal pups (14 females, 8 males) were killed on Sable Island in January 1981 to determine the presence and distribution of seal influenza virus and/or antibodies. Serum, lung, lymph node, and brain were collected and frozen within 4 ~ 6 h of death and stored at −20°C for up to 1 mo.

Beginning in late March 1981, numerous harp and a few hooded seals (*Cystophora cristata*) came ashore on Prince Edward Island and New Brunswick. The seals were in various states of health; many were dead. Of the 49 animals taken into captivity, most died or were euthanized. Tissue and/or blood samples for virus isolation were collected from 26 harp seals of various ages and one hooded seal pup.

In conjunction with a Department of Fisheries and Oceans sampling program in April 1981, lung and serum samples and swabs of oral mucosa were collected and frozen from up to 76 harp seals (6 adults, 35 subadults, 35 six- to seven-week old seals) and 6 hooded seal pups killed on the sea ice northeast of Newfoundland. Whole blood samples for antibody titers were held at 8–10°C for up to 3 h before being processed for serum and frozen at −20°C. All samples were stored at −70°C on return to Guelph.

Results

Laboratory Studies: Harp Seals

Inoculation with virus

There were no signs of disease in the harp seals inoculated

Table 1. Virus recovery and antibody titers from experimentally infected harp seals.

	Nasal washings[a]						Tissues[b]		Hemagglutination–inhibition antibody titer[c]			
Seal	Preinoculation	1d	2d	3d	6d	7d	Day killed	Virus recovery	1 wk	2 wk	3 wk	4 wk
A	–	–	–	–			2	None				
B	–	+	+				2	None				
C	–	–	–	+			3	Lung ($10^{3.5}$)				
D	–	–	–	+			3	Lung ($10^{3.5}$) bronchial lymph node (10^3)				
E	–	–	–	–	ND	–	7	None				
F	–	–	–	–	ND	–	7	None				
G	–	–	–	–	–	ND			–	1:160	1:80	–
H	–	–	–	–	–	ND			1:20	–	–	–

[a] +, virus recovered; –, no virus detected; ND, no data.

[b] Tissues examined included lung, brain, spleen, kidney, and colon and bronchial, gastric, and mandibular lymph nodes. Virus titers (in parentheses) are expressed as EID_{50}/mL organ suspension (approximately 1 g/mL).

[c] All blood samples prior to 1 wk were serologically negative.

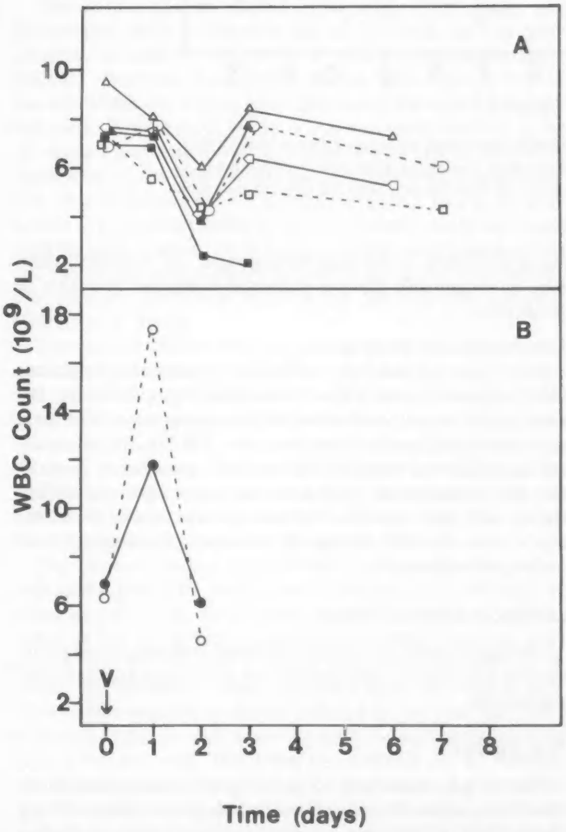

FIG. 1. White cell counts in eight harp seals inoculated with harbor seal lung homogenate (V). Six of the seals showed a pronounced decline in total white cell count, reaching the lowest values approximately 2 d after inoculation (A). The other two seals showed a marked increase in white blood cell count, which peaked approximately 24 h after inoculation (B). Virus was recovered from nasal washings and tissues of three seals (solid lines, closed symbols) and antibody from two seals (solid lines, open symbols). Uninfected seals are represented by broken lines and open symbols.

with the harbor seal lung homogenate. Six seals showed a gradual but pronounced decrease in the total white cell count (leukopenia), reaching the lowest value 2 d after inoculation (Fig. 1A). By the 3rd d, the white cell counts had returned to the normal range in all but one seal, which was euthanized. Two of the eight seals showed an increase in white blood cell count within 24 h after inoculation; thereafter, values returned to normal (Fig. 1B). In almost all cases, the elevation or decrease in total white cell counts reflected an equivalent rise or fall in the number of each cell type; there was no pattern related specifically to the granulocytic and mononuclear cell types.

We recovered virus from nasal washings and tissues from three of the eight experimentally inoculated harp seals and detected antibodies in one animal at 1 wk and in another at 2–3 wk after inoculation (Table 1). Two of the seals from which virus was recovered at necropsy were those with the lowest white cell counts 2 d after inoculation.

At necropsy, the lungs showed areas of atelectasis adjoining the entrance of the mainstem bronchi. The extent of the lesions seemed to be correlated with the interval following inoculation. There was mild atelectasis after 2 d, more extensive after 3 d in the two seals from which virus was recovered, and most evident in one of the two seals killed at 6 d. Though there were no overt signs of pneumonia, there were microscopic lesions of atelectasis, necrotizing bronchitis, and alveolitis.

We recovered a mycoplasma from the mouths of three of six seals at necropsy. The organism was not serologically related to that in the inoculum, and no further attempt was made to characterize it.

Inoculation with virus and mycoplasma

Four harp seals were first inoculated with a pure culture of mycoplasma M4359 and then with two doses of lung homogenate containing both virus and mycoplasma 4 d and again 5 d later. There were no significant clinical signs of disease in any of the seals. Three of the four showed a 60–100% increase in total white cell count 24 h after inoculation with mycoplasma. Thereafter, the cell counts returned to normal by day 4 when the seals were given the first inoculation of lung homogenate. Two of these seals responded with a 49 and 56% increase in white cell count on the following day; the third animal showed no response (Fig. 2). There was no additional increase in white cell count following the second inoculation with lung homogenate on day

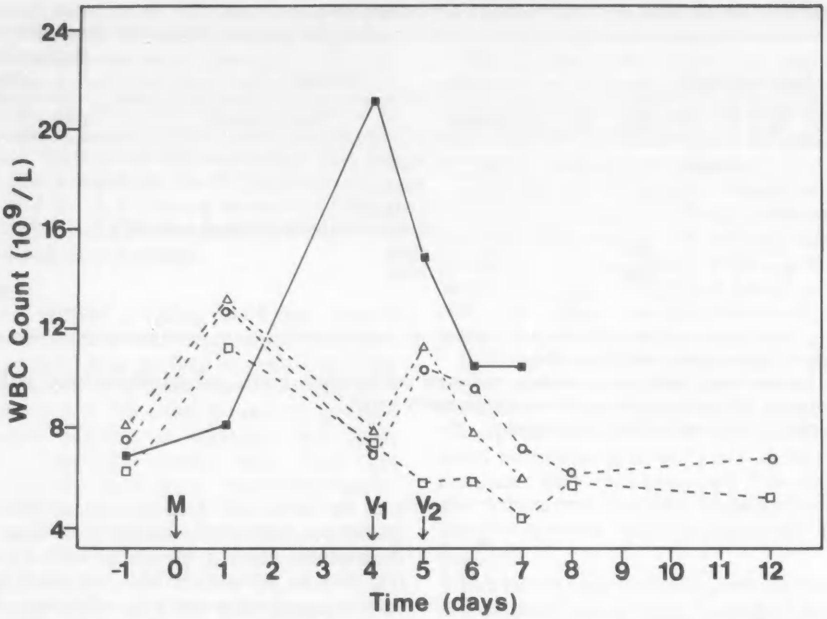

FIG. 2. White cell counts in four harp seals experimentally inoculated with mycoplasma M4359 (M), followed by two inoculations with harbor seal lung homogenate containing virus and mycoplasma (V_1, V_2). At necropsy, virus and mycoplasma were recovered only from the seal with the most pronounced white cell elevation.

5; by days 6–7, the counts of the three seals were normal. No virus or mycoplasma was recovered from any of these animals.

The fourth seal showed a more dramatic response in white cell count. There was no immediate response (24 h) to the mycoplasma inoculation. However, 4 d later, at the time the seal received the first dose of lung homogenate, the count was 165% above normal. It declined steadily but was still 30% above preinoculation levels when the seal was killed on day 7 (Fig. 2). Virus was isolated from its lungs (concentration 10^1 EID_{50}/g) and mycoplasma M4359 was consistently isolated from nasal swabs. At necropsy, there were mild lung lesions similar to those observed in the harp seals receiving a single inoculation of lung homogenate. The severity of the lesions was not correlated with the interval after exposure.

Laboratory Studies: Grey Seals

Inoculation with virus

There was no obvious sign of respiratory disease in any of the six grey seals inoculated with the harbor seal lung homogenate containing virus and mycoplasma. A mild serous to mucoid ocular and nasal discharge was noted in three of the seals. At the beginning of the experiment, total white cell counts were within a wide range. Within 1–2 d after inoculation, five of the six seals showed a 40–91% increase (mean 67%) in white cell count, due largely to an elevation in neutrophils and to a lesser extent lymphocytes. Within 2–5 d thereafter, the white cell counts returned to preinoculation levels or below.

No virus was recovered from any swab or tissue taken from the seals throughout the 6-d experimental period, nor were antibodies detected in any serum samples. We isolated a mycoplasma variably and intermittently from the mouth, eyes, lungs, and nose of all six seals. It was serologically distinct from the mycoplasma in the lung homogenate. At necropsy, there were no remarkable gross or microscopic lesions indicative of pneumonia.

Inoculation with mycoplasma

Two grey seals inoculated with a pure culture of mycoplasma M4359 showed no clinical or hematologic signs of disease. We were unable to recover the inoculated mycoplasma from nasal and conjunctival swabs taken for up to 12 d. We did, however, culture a different mycoplasma from both seals before inoculation and intermittently thereafter from swabs of nasal, conjunctival, and oral mucosa. No attempt was made to further characterize the new isolate. At necropsy, the lungs of both seals appeared normal.

Laboratory Studies: Controls

The harbor seals inoculated with irradiated lung homogenate showed no clinical, hematologic, or pathologic signs of viral pneumonia.

Field Studies

The 99 grey seals and 14 harbor seals examined on Sable Island showed no clinical or gross pathological evidence of lung disease, and no virus was isolated from lung tissue. Antibodies to A/seal/Mass/1/80 influenza virus were found in three adult male grey seals, with hemagglutination–inhibition titers of 1:14, 1:15, and 1:80.

Of the 27 harp and hooded seal pups examined from Prince Edward Island and the New Brunswick coasts, most were emaciated, weak, and dehydrated. Some had scarcely been nursing for a few days before coming ashore. Lung samples were free of influenza virus, and there was no serologic evidence to indicate prior exposure or colostral transfer of antibody from the mother.

None of the 76 harp seals and 6 hooded seals sampled from the ice northeast of Newfoundland had antibody to influenza virus. Since there was no morphologic evidence of lung disease, virus isolation was not attempted from these samples. Lungs from 42 of the harp seals were cultured for mycoplasma; none was isolated. Of 37 mouth swabs cultured, 13 were positive for a mycoplasma that was not serologically cross-reactive with that cultured from pneumonic harbor seals during the epizootic.

Discussion

In these studies, grey seals inoculated with crude lung homogenate containing influenza virus A/seal/Mass/1/80 and mycoplasma M4359 were refractory to infection. They showed only mild transient shifts in white cell counts, and virus could not be recovered, suggesting little or no replication in that species. The seals were killed before any antibodies could be produced.

The harp seals responded differently. Their lungs had microscopic lesions characteristic of influenza such as were observed in naturally (Geraci et al. 1982) and experimentally infected (Webster et al. 1981) harbor seals. Six of the 12 inoculated showed a leukopenia that can be associated with viral infection (Schalm et al. 1975). Virus was recovered in 4 of the 10 animals necropsied and antibodies in 2 survivors, indicating replication of the virus in that species. However, hematologic and viral findings were not always correlated. In all, we were unable to reproduce disease as we had in harbor seals inoculated with the same material (Webster et al. 1981), and in neither case did any of the seals acquire an infection remotely resembling that observed in harbor seals during the influenza epizootic (Geraci et al. 1982).

The marked difference in severity between the experimental and natural infection is a feature of influenza viruses (Shope 1931; Easterday 1975). Usually, other biological or environmental factors synchronize with the virus to produce disease (Easterday 1975). We could not implicate any one factor with certainty in our study of the natural infection but suspected that concurrent respiratory infection with mycoplasma and the stresses of adverse environmental conditions might have driven the virus to full expression (Geraci et al. 1982).

The present studies suggest that the mycoplasma isolate (M4359) is part of the normal flora of harbor seals. When given alone to grey seals, M4359 was innocuous; together with the virus, it did not produce respiratory disease that was more severe than we observed with the virus alone (Webster et al. 1981). Furthermore, a study on harbor seals, the natural host, showed that respiratory disease induced by the virus alone was as severe as that in seals receiving lung homogenate containing virus (Webster et al. 1981) and mycoplasma (H. L. Ruhnke, unpublished data). Though we were unable to ascribe a role for mycoplasma, we have come to realize that it is prevalent, perhaps species specific, and not necessarily pathogenic, although an infection was established in one harp seal.

The virus replicated only in harbor and harp seals, both of the genus *Phoca*, and not in experimentally infected grey seals, suggesting that the influenza virus had not adapted to the genus *Halichoerus*. Yet, antibodies to the same surface antigens as A/seal/Mass/1/80 were found in three grey seals on Sable Island 650 km from the center of the original epizootic. There are at least three possible explanations for this finding. The few grey seals in the experiment may have been insufficient to test the full range of infectivity of the virus; a larger sample might have yielded different results. Second, the antibodies in the wild grey seals may have been induced by a related but different virus, one that was not visibly harmful to the population. And third, some of the grey seals on Sable Island may have been exposed to a large contaminating dose of virus, sufficient to induce an antibody response, without significant viral replication. In contrast with the grey seals, none of the free-ranging harp or hooded seals sampled had antibodies to the virus, indicating that they had not been exposed or that antibodies may be short lived, as we had found in laboratory seals that had been mildly infected.

In light of this and a previous study (Webster et al. 1981), it seems unlikely that the influenza virus A/seal/Mass/1/80 could indiscriminately cause widespread infection among seal populations. However, we cannot overlook the possibility that this virus could become pathogenic through genetic reassortment (Hinshaw et al. 1980) or appropriate biological and environmental triggers, particularly in other members of the genus *Phoca*, such as the harp and ringed seal, *P. hispida*. That such agents can be transferred sporadically to isolated seal populations is suggested by at least three occurrences in harbor seals (Bardarson 1931), crabeater seals, *Lobodon carcinophagus* (Laws and Taylor 1957), and grey seals (Gallagher and Waters 1964) of diseases strikingly similar to influenza, spanning three continents over a period of 50 yr. Now alerted to these events, we are expanding our vigilance. At the time of this writing we are encountering a three- to four-fold increase in the number of stranded harbor seals along the Massachusetts coast. Of 59 seals examined from January to April, 1982, most have died of acute pneumonia. A distinct avian influenza virus of the antigenic subtype H4N5 has been isolated from 13 of these seals (V. S. Hinshaw, unpublished data).

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Body and Fin Form and Strike Tactics of Four Teleost Predators Attacking Fathead Minnow (*Pimephales promelas*) Prey

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Webb, P. W. 1984. Body and fin form and strike tactics of four teleost predators attacking fathead minnow (*Pimephales promelas*) prey. Can. J. Fish. Aquat. Sci. 41: 157–165.

Experiments with teleosts attacking fathead minnow (*Pimephales promelas*) prey showed that piscivore locomotor tactics vary with body/fin morphology. Predators were tiger musky (*Esox* sp.), rainbow trout (*Salmo gairdneri*), smallmouth bass (*Micropterus dolomieui*), and rock bass (*Ambloplites rupestris*) representing several morphological series from more flexible to more rigid bodies, elongate to gibbose bodies, soft-rayed to acanthopterygian median/paired fin patterns, and more to less myotomal muscle. Two predicted optimal tactics were common to the four predators: (1) strike at the prey center of mass and (2) strike prey from the side. Other tactics varied among the predators. Tiger musky always used S-start fast-starts, rainbow trout used steady swimming with body/caudal fin movements, and smallmouth and rock bass used steady swimming with body/caudal fin movements for closer prey and started attacks on distant prey with pectoral propulsion. Tiger musky overshot prey, this being prevented by the use of paired fins as brakes in the two centrarchids. Rainbow trout regularly chased prey, but effective braking coupled with suction feeding appeared to make chases less necessary for smallmouth and rock bass. Speeds in strikes increased according to rock bass < smallmouth bass < rainbow trout < tiger musky consistent with expectations based on morphology. Each species used attack speeds likely to minimize closure times, which is the general optimal strategy for interceptors. Tiger musky attacked at maximum speeds but rainbow trout and smallmouth and rock bass attacked at speeds very much lower than their maximum potential. The prey has a low response threshold for these three species compared with tiger musky when high speeds and associated large prey reaction distances would increase closure times.

Des expériences avec des téléostéens attaquant des têtes-de-boule (*Pimephales promelas*) ont montré que les tactiques locomotrices des piscivores varient selon la morphologie du corps et des nageoires. Les prédateurs étaient le maskinongé (*Esox* sp.), la truite arc-en-ciel (*Salmo gairdneri*), l'achigan à petite bouche (*Micropterus gairdneri*) et le crapet de roche (*Ambloplites rupestris*), représentant plusieurs séries morphologiques allant de corps plus flexibles à plus ridiges, de corps allongés à bossus, de structures de nageoires formées de rayons mous à des nageoires paires médianes de type acanthoptérygien, et des muscles plus ou moins myotomiques. Deux tactiques optimales prédites étaient communes aux quatre prédateurs : (1) attaque au centre de masse de la proie et (2) attaque de la proie par le côté. Les autres tactiques différaient selon les prédateurs. Le maskinongé utilisait toujours des départs rapides en S, la truite utilisait une nage constante avec des mouvements du corps et de la nageoire caudale, alors que l'achigan et le crapet de roche se servaient d'une nage constante avec des mouvements du corps et de la nageoire caudale pour les proies plus proches et amorcaient des attaques contre les proies éloignées en se propulsant au moyen de leurs nageoires pectorales. Le maskinongé dépassait la proie, ce qui ne se produisait pas chez les deux centrarchidés à cause de l'utilisation de nageoires paires comme freins. La truite poursuivait régulièrement la proie, mais le freinage efficace associé à l'alimentation par succion semblaient rendre les poursuites moins nécessaires pour l'achigan et le crapet de roche. Les vitesses d'attaque étaient plus grandes suivant la séquence crapet de roche < achigan < truite < maskinongé en accord avec les prévivions basées sur la morphologie. Chaque espèce utilisait des vitesses d'attaque vraisemblablement pour minimiser le temps d'approche, ce qui est la stratégie générale optimale pour les intercepteurs. Le maskinongé attaquait à des vitesses maximales, mais la truite, l'achigan et le crapet de roche attaquaient à des vitesses beaucoup plus faibles que leur potentiel maximal. La proie a un seuil de réponse faible pour ces trois espèces à comparer au maskinongé alors que des vitesses élevées et les distances associées de réaction des grosses proies augmenteraient le temps d'approche.

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The boundaries on permissible behavioral options for an animal are set by the functional properties of its morphology and physiology (Bennett 1980). On this basis, Webb and Skadsen (1980) used hydromechanical principles to predict optimal strike tactics for tiger musky (*Esox* sp.) attacking fish prey. The optimal tactics were (1) strike at the prey center of mass, (2) strike the prey from the side, and (3) strike as rapidly as possible in order to close with prey in the least time. Striking at the center of mass from the side of the prey is predicted to be optimal because the center of mass moves least during initial stages of an escape and at an angle tending towards a right angle as measured from the initial prey stretched straight position or swimming path. Then striking at this target from the side anticipates the most probable escape trajectory (Webb and

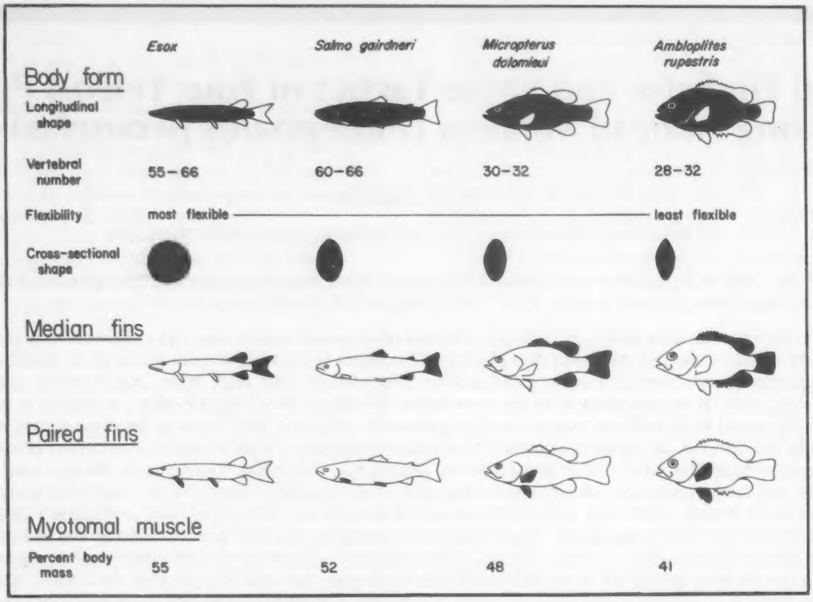

FIG. 1. Summary of functional and morphological features of four teleost piscivores (see text for details).

Skadsen 1980). Striking rapidly is the most obvious general solution for any interception game to minimize the duration of an interaction (Isaacs 1975; Weihs and Webb 1983). In fish attacking other fish, the greatest distance is covered in the least time by accelerating towards prey. Maximum acceleration is achieved in fast-starts. In order to aim at specific targets, however, "S-starts" should be used in which the body is bent into two large amplitude flexures or S shapes (Webb and Skadsen 1980; Rand and Lauder 1981). The ability to use S-starts depends on body flexibility and will be affected by morphological features such as body shape and vertebral number. Therefore, many fish will be unable to achieve all of the apparently optimal tactics found for esocids.

My purpose was to determine how strike tactics varied among four teleost predators with different body forms and hence locomotor capabilities. It was postulated that strike targets and approach angles should not differ among predators and that locomotor patterns would shift from fast-starts in more flexible species to slower chases in less flexible species.

Methods

Predators and Prey

The four predators were as follows: tiger musky (*Esox* sp; hybrid male *E. lucius* × female *E. masquinongy*; total length $L \pm 2$ SE $= 23.6 \pm 1.0$ cm; mass $M \pm 2$ SE $= 51.09 \pm 6.94$ g), rainbow trout (*Salmo gairdneri*; $L = 25.0 \pm 1.8$ cm; $M = 165.02 \pm 20.24$ g), smallmouth bass (*Micropterus dolomieui*; $L = 23.6 \pm 1.4$ cm; $M = 184.53 \pm 30.00$ g), and rock bass (*Ambloplites rupestris*; $L = 15.1 \pm 1.9$ cm; $M = 61.91 \pm 23.08$ g). Tiger musky, rainbow trout and smallmouth bass were obtained from hatcheries and rock bass were seined from a local stream.

The four freshwater species include fish in their diet and represent a range of locomotor capabilities in the following areas; (1) body/caudal fin (BCF) transient propulsion as used in fast-starts and powered turns, (2) body/caudal fin periodic propulsion used in cruising and sprints, and (3) median and paired fin (MPF) propulsion characteristic of low-powered slow swimming, precise maneuver, and braking. Functional and morphological features are summarized in Fig. 1 and relative performance expectations in Table 1.

The basis for selection of body/fin morphologies (Table 1; Fig. 1) was as follows. Tiger musky have a very flexible elongate tubular body (Keast and D. Webb 1966) that can bend into large S shapes for acceleration strikes (Webb and Skadsen 1980; Rand and Lauder 1981). The caudal area is enhanced by the posterior location of dorsal and anal fins that would also improve thrust for acceleration (Webb 1977). The pectoral and pelvic fins are ventrolateral where their use in braking and maneuver is least effective (Alexander 1967; Gosline 1971, 1980). Esocids lack myotomal red muscle so that sustained chases cannot occur (Boddeke et al. 1959; Johnson 1983).

Rainbow trout have a somewhat elongate but fusiform body, large vertebral number, and good flexibility to bend into double flexures (Webb 1976). Depth is enhanced near the center of mass by the dorsal fin that should result in greater stability during turning compared with tiger musky. There is substantial red and pink muscle to sustain chases (see Johnston 1983). Caudal area is enhanced by the anal fin. Paired fins are similar to those of tiger musky.

Smallmouth bass have a compressed fusiform body but a low vertebral number (30–32) and insufficient flexibility to bend into large-amplitude S postures. The body is slightly more compressed than rainbow trout, with a more pointed elliptical cross-section. Together with the extensive dorsal and anal fins the body provides for greater turning stability, smaller turning radius (Howland 1974; Webb 1983), and diodontiform propulsion (Lindsey 1978). As in other acanthopterygians, the pectoral fins are lateral and the pelvics are located ventrolater-

TABLE 1. Comparison of relative capabilities expected for four teleost predators with respect to locomotor performance in strikes against fish prey.

	Tiger musky	Rainbow trout	Smallmouth bass	Rock bass
Kinematic pattern in fast-starts	S-starts and C-starts	S-starts and C-starts	C-starts	C-starts
Effectiveness of fast-start in reaching specific targets at maximum acceleration	Good	Good	Poor	Poor
Relative performance in body/caudal fin cruising and sprints (chases)	Poor	Good	Good	Poor
Relative maneuverability during strikes/chases and braking	Poor	Poor	Good	Good

ally beneath (Rosen 1982) for labriform propulsion and braking. In addition, suction mechanisms are more sophisticated (Lauder 1982).

Rock bass, in the same family as smallmouth bass, have the same paired fin patterns. The major differences are in body form. The body is short, the vertebral number 28–32, and hence the fish is the least flexible of the species studied here. The body is more compressed than the other species and the shape is gibbose (Keast and Webb 1966); the form is that usually associated with high maneuverability at low speed (Alexander 1967; Gosline 1971; Webb 1982a). However, the large surface area would be expected to result in large drag for BCF periodic motions (Weihs and Webb 1983), so chases would be expected to be rare.

Prey were fathead minnows (*Pimephales promelas*). Length and mass were measured from a subsample of 50 prey taken from stocks used in the experiments ($L = 5.5 \pm 0.2$ cm; $M = 1.02 \pm 0.14$ g). The prey were obtained from local bait stores.

Fish were held in the laboratory for more than 1 wk for prey and more than 3 wk for predators. Predators were fed fathead minnows to ensure familiarity with the prey. Holding conditions were the same as experimental conditions of continuous illumination ($0.2\ \mathrm{mW \cdot m^{-2}}$), a temperature of 15°C, and dissolved oxygen at air saturation levels.

Experimental Procedures

Individual predators were starved for 1 wk to ensure high feeding motivation. Single predators were placed in one of two observation arenas. The first was 50 cm square and 10 cm deep, described in detail by Webb and Skadsen (1980). The second arena was roughly an oval 200 cm long and 150 cm wide, filled with water to a depth of about 15 cm. It was used in case the smaller arena influenced behavior substantially. It was found that trout in particular cornered prey against edges in either the small arena or in the large arena. Further increases in arena size were judged unlikely to be effective in eliminating such use of corners and edges by trout. Tactics of the other four predators, which used edges infrequently, were not influenced by the size of the arena. Since arena size did not influence tactics, results reported here are combined for the two arenas.

Predators were acclimated to an arena overnight. The next day a single prey was introduced via a water-filled cup through one of four side-ports (diameter 2.5 cm) selected at random. As prey were eaten, additional prey were added.

Predator–prey interactions were recorded on videotape. Tape was analyzed "frame-by-frame" (framing rate 60 Hz). Predator strike patterns were recorded and the following state variables were measured at various predator decision points: (1) distance separating predator and prey, (2) predator speed, (3) prey speed, and (4) angle between prey body axis and the predator strike path. Predators were required to make decisions at the following events of a predator–prey interaction: (i) at initiation of a strike, (ii) at a prey response to an attack, and (iii) in terminating an interaction. Mean values of state variables were calculated for predator activities. Finally, the predator target was defined as either the point along the prey's body struck by the predator or the point where the strike path would have intersected the body had the prey not evaded the predator's strike.

Results

Predator Strikes

The beginning of a strike was defined by the predator starting to move towards the prey. Stationary prey were usually attacked soon after they stopped swimming, and such strikes represented 76% of all attacks on prey. Rainbow trout usually attacked moving prey (Fig. 2), usually on sight, while the other three predators usually waited, presumably for a favorable opportunity.

Tiger musky and rainbow trout used BCF propulsion exclusively (Fig. 2) but the former employed transient patterns in acceleration S-starts, while rainbow trout used BCF periodic propulsion movements. No S-starts were seen in rainbow trout in spite of their ability to accelerate in this way (Webb 1976).

Smallmouth and rock bass rarely used fast-starts in strikes, and when they occurred, C-starts were used. Instead, these predators usually used either BCF periodic of MPF propulsion, mainly pectoral fin swimming in attacking prey. When used, pectoral propulsion merged with, and often overlapped, BCF propulsion, which was used as the predators closed with the prey. The body moved continuously on a given strike trajectory during the change from pectoral to caudal swimming. The continuity of the approach provided no justification for describing the pectoral phase as a "stalk," separate from the BCF periodic propulsion phase. Thus, stalks were actually very rare in the homogenous observation arenas used in these experiments.

Significant differences (t-test, $\alpha = 0.05$) were not found in distances or angles of strikes made at stationary versus moving prey (Table 2), except for rock bass, which attacked moving prey from smaller distances. Similarly, no consistent relationships were found relating prey motion and predator strike speeds (Table 2). The general absence of differences between tactics for moving and stationary prey may relate to the temporary nature of prey stationary periods.

Tiger musky struck at prey over the shortest distances, averaging about 7.5 cm ($0.32\ L$), as observed for other esocids (Webb and Skadsen 1980; Rand and Lauder 1981). Rainbow

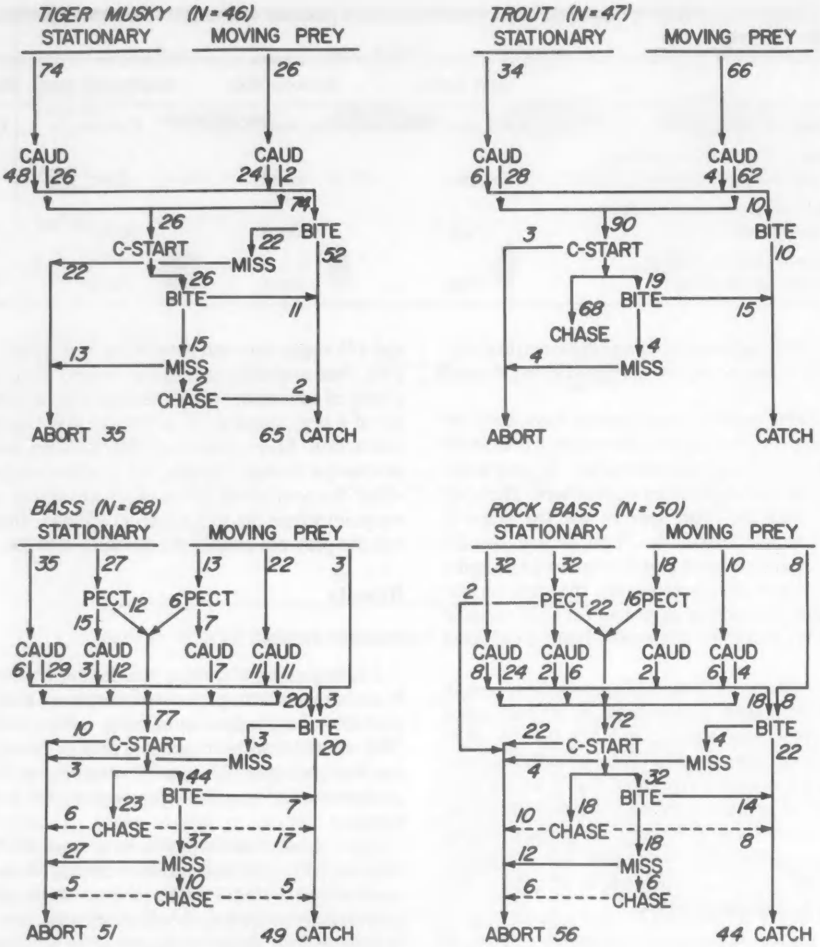
TIGER MUSKY (N=46)
STATIONARY
MOVING PREY
74
26
CAUD
48
26
CAUD
24
2
74
26
BITE
22
52
C-START
22
MISS
26
BITE
11
15
13
MISS
2
2
CHASE
ABORT 35
65 CATCH
TROUT (N=47)
STATIONARY
MOVING PREY
34
66
CAUD
6
28
CAUD
4
62
10
90
BITE
3
C-START
10
19
68
BITE
15
CHASE
4
4
MISS
ABORT
CATCH
BASS (N=68)
STATIONARY
MOVING PREY
35
27
13
22
3
PECT
12
6
PECT
15
7
CAUD
CAUD
CAUD
CAUD
6
29
3
12
7
11
11
20
3
77
BITE
10
C-START
3
20
MISS
3
44
BITE
6
23
7
CHASE
37
17
27
MISS
5
10
5
CHASE
ABORT 51
49 CATCH
ROCK BASS (N=50)
STATIONARY
MOVING PREY
32
32
18
10
8
2
PECT
22
16
PECT
CAUD
CAUD
CAUD
CAUD
8
24
2
6
2
6
4
18
8
72
BITE
22
C-START
4
22
MISS
4
32
BITE
10
18
14
CHASE
18
8
12
MISS
6
6
CHASE
ABORT 56
44 CATCH

FIG. 2. Flow charts of events and their frequency during predator–prey interactions between four teleost predators and fathead minnow prey. *N* is the total number of interactions analyzed. Chases by rainbow trout may have been influenced by walls and hence are not analyzed. For this reason, the flow diagram for rainbow trout must be left incomplete. CAUD, caudal fin swimming; CHASE, chase; C-START, prey response, usually a C-start acceleration maneuver.

trout struck at prey over the longest distances, averaging 20–25 cm (0.8–1.0 *L*), and smallmouth and rock bass were intermediate, striking from 8 to 16 cm (0.34–1.0 *L*) from the prey (Table 2).

Tiger musky struck at the highest speeds, average values being about 65 $\mathrm{cm \cdot s^{-1}}$ (2.8 $L \cdot \mathrm{s}^{-1}$). The highest speeds of the other three predators also occurred during BCF propulsion. Smallmouth bass averaged speeds of about 40 $\mathrm{cm \cdot s^{-1}}$ (1.7 $L \cdot \mathrm{s}^{-1}$) in attacking moving prey, and similar speeds were observed for rainbow trout attacking moving prey and rock bass attacking stationary prey. Rainbow trout and rock bass differed in that the former attacked stationary prey at lower speeds, but rock bass was slower while attacking moving prey (Table 2). Speeds of smallmouth and rock bass during pectoral fin propulsion were about 7–11 $\mathrm{cm \cdot s^{-1}}$ (up to 0.7 $L \cdot \mathrm{s}^{-1}$), substantially lower than BCF swimming speeds, except for rock bass attacking moving prey. Strike angles did not vary significantly among the predators or with the different swimming patterns (Duncan's multiple range test, $\alpha = 0.05$).

Predator Response to Responding and Nonresponding Prey

A predator initiates an attack, but the next event depends on prey behavior. Prey may respond with either a low-intensity (low speed, small turning angle) or a high-intensity evasive maneuver or they may not respond until the predator makes contact (Webb 1982b). Since predators probably cannot judge prey response levels in advance, predator decisions are considered only in terms of responding versus nonresponding prey.

Predators always attempted to bite and capture nonresponding prey. Nonrespondents were most common in 74% of strikes by tiger musky (Webb 1982b) but this predator was least successful in catching 70% of these prey (Fig. 2). The other three predators captured 82–100% of nonresponding prey, although these represented only 10–26% of prey attacked. In

TABLE 2. State variables for predators and prey at the start of various predator behaviors during strikes on fathead minnow prey. d = distance (cm) separating the predator and prey; θ = angle (degrees) between predator strike trajectory and the prey body long axis; U_{pred} = initial predator swimming speed ($cm \cdot s^{-1}$); U_{prey} = initial prey swimming speed ($cm \cdot s^{-1}$); $\bar{U}_{pred}$ = mean predator swimming speed ($cm \cdot s^{-1}$); $\bar{U}_{prey}$ = mean prey swimming speed ($cm \cdot s^{-1}$). Data are $\bar{X}$ ± 2 SE. Sample sizes are obtained from Fig. 2.

	Tiger musky	Rainbow trout	Smallmouth bass	Rock bass
Strikes at stationary prey				
Predator caudal swimming				
d	7.1±1.6	26.1±7.1	14.4±3.5	12.6±4.8
θ	84±20	91±20	75±18	84±22
U_{pred}	0	0	0	0
U_{prey}	0	0	0	0
$\bar{U}_{pred}$	64±9	22±13	46±13	36±15
$\bar{U}_{prey}$	0	0	0	0
Predator pectoral swimming				
d	—	—	22.5±6.4	17.0±5.4
θ	—	—	64±20	71±20
U_{pred}	—	—	0	0
U_{prey}	—	—	0	0
$\bar{U}_{pred}$	—	—	7±3	9±4
$\bar{U}_{prey}$	—	—	0	0
Strikes at moving prey				
Predator caudal swimming				
d	7.6±1.7	19.5±6.1	15.8±4.5	8.4±2.7
θ	103±24	97±24	91±21	71±70
U_{pred}	0	0	0	0
U_{prey}	24±8	31±19	20±5	9±3
$\bar{U}_{pred}$	54±18	47±12	35±10	13±9
$\bar{U}_{prey}$	24±8	31±17	23±3	16±11
Predator pectoral swimming				
d	—	—	21.1±8.9	23.7±7.8
θ	—	—	99±25	65±44
U_{pred}	—	—	0	0
U_{prey}	—	—	12±9	9±9
$\bar{U}_{pred}$	—	—	11±7	10±4
$\bar{U}_{pred}$	—	—	11±9	7±5

these experiments, the predators did not chase prey that were missed but aborted the attacks. These misses represented from 30% of catch attempts by tiger musky to 0% by rainbow trout and are attributed to intrinsic predator errors (Nyberg 1971). Such errors are known to occur at higher frequencies with increasing speed of an event and as the required motor force increases (Schmidt et al. 1979). Thus, tiger musky would be expected to make more errors because it used faster, high-power movements.

Predators responded to escape attempts by prey in one of three ways: (1) attempt a bite and capture, (2) chase, and (3) abort the attack. A failure to catch prey with a bite was followed by either a chase or abortion of the attack (Fig. 2). Tiger musky attempted to bite and capture all prey, while smallmouth bass attempted to bite 57% of respondees, rock bass 44%, and rainbow trout only 21%. A series from tiger musky through rainbow trout and smallmouth to rock bass is one from zero aborted strikes in tiger musky to 31% abortions in rock bass. Chases increased from none by tiger musky to 76% of predator responses to responding prey by rainbow trout, with the two centrarchids being intermediate and chasing about 27% of escapees.

There was a marked difference in locomotor behavior between the soft-rayed and spiny-rayed predators at the decision point forced by prey responding to a strike. Tiger musky overshot the prey position, and as they were accelerating rapidly, overshooting took tiger musky out of reasonable position to continue the interaction. Rainbow trout invariably turned to follow the prey. Here, the large reaction distance of fathead minnow to strikes by rainbow trout (Webb 1982b), and lower speeds of attacking rainbow trout compared with tiger musky, probably gave time for rainbow trout to respond once a prey was committed to an escape path by its avoidance maneuver.

The two centrarchids usually used their paired fins as brakes as the mouth opened. They did not, therefore, overshoot the target and were ideally situated to follow fleeing prey.

In general, these observation, together with those on the initiation of strikes, show that the tiger musky is a lunge/biter. The rainbow trout, although having the functional and morphological capacity to lunge, is actually almost entirely a chaser under the conditions of the experiment. The two centrarchids are more complex. The nonlunging approach behavior is similar to rainbow trout and the tendency to bite at prey is similar to tiger musky; they are best considered intermediate.

State variables associated with predator decisions to bite, chase, or abort are shown in Table 3. No differences were found in speeds or distances associated with chases or aborts except for

TABLE 3. Speeds of predators (U_{pred}, cm·s^{-1}) and prey (U_{prey}, cm·s^{-1}) and distance separating the fish (d, cm) at the start of a prey response to a strike associated with the three predator behavior choices.

	Tiger musky	Rainbow trout	Smallmouth bass	Rock bass
Predator bites at prey				
d	2.0±1.0	6.7±3.3	4.9±0.9	3.9±1.2
U_{pred}	99±24	43±15	56±14	43±37
U_{prey}	80±25	75±20	66±19	44±13
Predator chases prey				
d	5.4	8.2±2.0	7.5±2.2	6.9±1.6
U_{pred}	66	39±9	27±10	10±3
U_{prey}	38	54±9	48±13	39±10
Predator aborts prey				
d	—	9.3	7.0±3.2	6.3±2.4
U_{pred}	—	86	30±12	6±3
U_{prey}	—	87	65±20	30±13

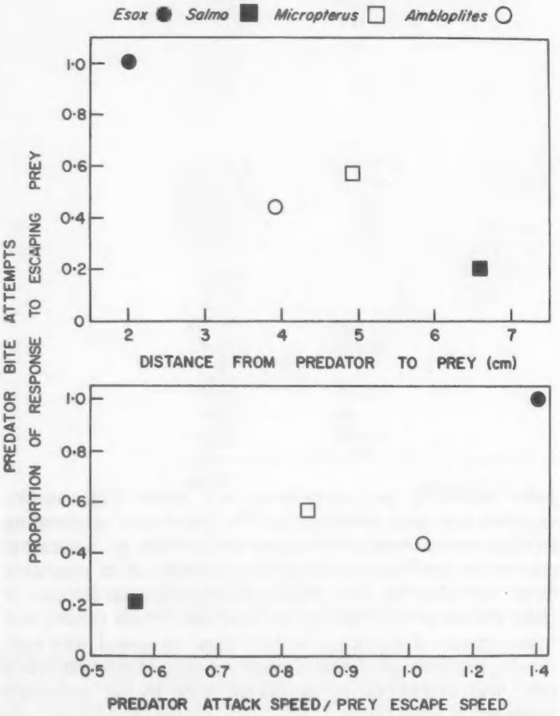

FIG. 3. Relationship between the frequency of bites at responding prey in relation to separation distance between the predator and prey at the start of a bite and to relative speed (U_{pred}/U_{prey}) for the four predators.

rock bass, which aborted strikes when swimming slowly. In general, the decision to chase or abort could not be attributed to the variables measured. Chases by rainbow trout were not further analyzed because it was not certain to what extent walls influenced their behavior.

Bites occurred most frequently when prey were approached more closely and when the speed ratio between predator and prey was larger, with predator speed approaching or exceeding prey speed. (Fig. 3). Thus, the decision to bite appears to be determined by how far away the prey are located and their speed relative to the predator.

Tiger musky and smallmouth and rock bass did not always abort an interaction when a bite at responding prey failed during a chase, contrasting with the initial stages when all failures were aborted. The majority of failures (67% by rock bass, 73% by smallmouth bass, 87% by tiger musky, 100% by rainbow trout) were aborted. The remainder resulted in further chases, usually ending after a single additional attempt to capture prey, although up to four bite attempts in a single chase were recorded for smallmouth bass. Since the numbers of observations were so small for these relatively rare events, details are not presented. In general, chases were not very successful for the predator.

Targets

The target was defined at the intersection of the strike trajectory with the prey's body. Results are summarized in Table 4. Such targets ranged along the whole body length but were clustered near the vicinity of the center of mass, the predicted optimum. While fish cannot identify the center of mass as a discrete point, it is associated with other morphological features that could act as "target cues" such as the maximum depth, eyes, fins, etc. (Houssay 1912; McPhail, 1977; Webb and Skadsen 1980).

Discussion

A predator may vary four principal tactical components; target, strike angle, closure rate, and maneuver. Target and strike angle need not depend on locomotor morphology, while speed and maneuverability are dependent (see Webb 1982a, 1983; Weihs and Webb 1983). Thus, in the present experiments, the two components of strike angle and target, which should be independent of locomotor morphology, were indistinguishable for the various predators. Furthermore, the mean values for targets and strike angles were optimal in terms of

TABLE 4. Strike tactics measured for four species of teleost predators attacking fathead minnow prey. Means ± 2 SE are shown.

Predator	Target (distance from nose/prey body length)
Tiger musky	0.31±0.04
Rainbow trout	0.34±0.08
Smallmouth bass	0.37±0.04
Rock bass	0.39±0.04
Prey center of mass	0.35±0.05

predictions based on the likely target escape trajectories, as found in previous studies on tiger musky (Webb and Skadsen 1980; Rand and Lauder 1981). Nevertheless, other factors may influence choice of target and strike angles, negating the importance of the kinematic principles. For example, Deelder (1951) and Hoogland et al. (1956) report that perch (*Perca fluviatilis*) maneuver to take prey by the head, apparently because they are less effective at turning prey than other predators such as *Esox*. Furthermore, predators are opportunistic. Although predators may usually attack from the side and usually at a target about one third along the body length from the head, the observations span the whole range of possible values as opportunities occur.

Body/fin morphologies should influence locomotor options of speed and maneuver in prey capture. The optimal tactic of using S-starts to close with prey in minimal time is characteristic of esocids, as observed here and elsewhere (see Webb and Skadsen 1980; Rand and Lauder 1981; Weihs and Webb 1983). However, the high rate of acceleration results in frequent overshooting of prey and possibly reduces success of lunges, as seen by relatively low success in catching nonresponding prey (Schmidt et al. 1979). The primitive ventrolateral position of the paired fins prevents effective braking. Therefore, the S-start strike tactic is actually optimal only for the initial stage of an attack and must be considered suboptimal if an extended interaction is likely. Hence, the important corollary of the lunge tactic is that prey should normally be intercepted before an escape maneuver can develop (Webb and Skadsen 1980) and hence is effective only if prey response thresholds are high (Webb 1982b).

Rainbow trout have the capability to employ S-starts but these were not seen in prey capture. Since prey response thresholds are low for rainbow trout (Webb 1982b), the effectiveness of a fast-start strike tactic is greatly diminished because extended interactions are inevitable. The two centrarchids lack the body flexibility to use fast-starts. The alternative C-starts cannot be used effectively to strike at specific targets anywhere in space because unbalanced lateral forces cause the body to recoil (Weihs 1973). As a result, the strike trajectory of a C-start begins at an angle to the initial axis. Such recoil can be corrected by repeating the initial body-bend typical of fast-starts and powered turns (Weihs 1972). However, such a maneuver results in loss of momentum, such that effective net forward motion can stop (Webb 1976). Clearly, such a maneuver to correct for C-start recoil would delay effective motion towards the prey and at the same time would be associated with substantial motion that would undoubtedly elicit a prey escape maneuver. Therefore, rainbow trout and smallmouth and rock bass must use other strike tactics not based on fast-starts.

Rainbow trout chased their prey. For this species the larger lateral projected area compared with tiger musky would make them more maneuverable (Webb 1983) and hence mechanically more proficient to extend an interaction in a chase. Overshoot is generally less of a problem because prey reaction distances are large and speeds are lower than for tiger musky, providing rainbow trout with more time to maneuver after the prey commits itself by an escape response. In general, chases by the other three predators, tiger musky and smallmouth and rock bass, were relatively infrequent responses to prey avoidance attempts, and a response was often sufficient to deter a predator (Fig. 2; Webb 1981). Thus, chases by rainbow trout may be unexpected, with success being based on prey expectations of infrequent chases by other piscivores.

Smallmouth and rock bass have larger body and median fin areas than rainbow trout due to the posterior expansion of their dorsal and anal fins. This facilitates greater maneuverability through smaller turning radii (Webb 1983), which would be expected to favor chases. In contrast, the larger area, especially caudally, would increase drag (Lighthill 1975; Webb 1977), and the more compressed body compared with rainbow trout is associated with less myotomal muscle (Webb 1978).

Thus, in comparing the occurrence of chases among the three fusiform species, chases were more common in a series, rainbow trout > smallmouth bass > rock bass, and hence inversely correlated with body/fin area and directly correlated with lateral flattening and the proportion of myotomal muscle.

The two centrarchids have two features that may also contribute to the relatively low number of chases and absence of sustained chases. These features are effective brakes and suction. Brakes minimize overshoot (Harris 1937) and hence reduce the distance separating the predator and its prey when the latter responds. Suction allows extension of the bite without body translocation (Lauder 1983).

The general expectations concerning morphology and prey capture abilities are thus reasonably well supported. Along a series from tiger musky through rainbow trout and smallmouth bass to rock bass, fast-starts are replaced by swimming strikes with body movements like those used in steady swimming. Increased use of MPF propulsion for the initial movements is seen in the centrarchids, plus braking and better positioning to attack fleeing prey. Suction is probably the most crucial adaptation.

Measured speeds also fit expectations. Along the same series, strike speeds generally decreased. However, except for tiger musky (Webb and Skadsen 1980), performance is submaximal. For example, 25-cm-long rainbow trout and smallmouth bass should be capable of maximum sprint speeds of the order of 300 $cm \cdot s^{-1}$ (Wardle 1975; Wardle and Videler 1980), at least seven times faster than observed. Similarly, the maximum acceleration performance characteristic of tiger musky was absent in strikes by the other predators. In general, maximum performance would be expected to minimise strike times and hence the duration of an interaction, as required to satisfy the general optimal strike strategy for interceptors (Isaacs 1975).

In practice, this general strategy of minimizing interaction times when prey respond can be achieved only when maximizing speed and/or acceleration does not increase prey reaction distances faster than the prey can tranverse that distance. Thus, an expected closure time can be defined as the predator speed at the time of a prey response divided by prey reaction distance. This closure time should be minimized by the predator to achieve an interceptor's general optimal strike strategy of minimizing interaction time. In practical terms, this returns to the optimal tactical component that a predator should attempt to intercept prey before a prey response displaces the target substantially from the predtor's strike trajectory.

It follows that maximizing speed and/or acceleration can only be an appropriate tactic for a predator if prey reaction distance increases proportionately with speed. However, when closure times would be expected to be independent of speed, consideration of the escape stimulus for the prey shows this may not occur. Commonly, the escape stimulus is the rapid enlargement of the visual image of an approaching predator, the looming effect (see Gibson 1979; Lythgoe 1979). It is measured as the rate of change of the angle α subtended by the predator's silhouette (Dill 1973, 1974a; Webb 1981):

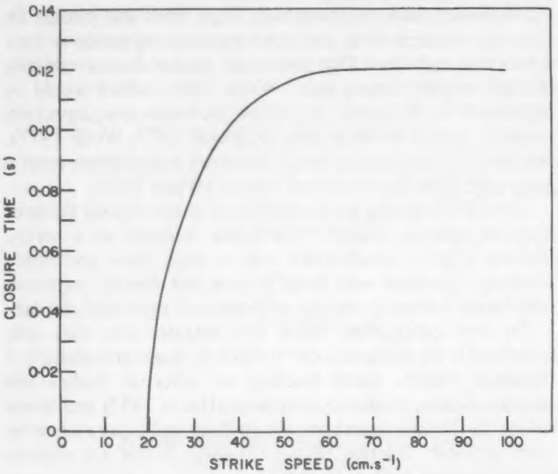

FIG. 4. Relationship between closure time and constant predator attack speed calculated from eq. 1 using a prey response threshold value of 1.5 rad·s^{-1} for trout-like and bass-like predators with S = 4 cm, located 9 cm behind the nose.

$$(1) \quad \frac{d\alpha}{dt} = \frac{4\,U_{\mathrm{pred}}\,S}{4d^2 + S^2}$$

where S is the mean value of the predator maximum depth and width, U_{pred} is the predator speed, and d is the distance between the prey and the predator's maximum cross-sectioned silhouette (about 9 cm behind the nose for the predators used here).

Equation 1 can be used to calculate reaction distances for various U_{pred} and hence closure times if $d\alpha/dt$ is known. A typical value of $d\alpha/dt$ for fathead minnow prey responding to attacks was calculated from Webb (1982b) to be 1.5 rad·s^{-1}. This value differs from maximum likelihood values for a population of respondants and nonrespondants and averages over different prey response patterns. The average value was used because a predator only has to respond to respondants but does not know which response pattern will occur. The value of $d\alpha/dt$ of 1.5 rad·s^{-1} was used to calculate reaction distances at various swimming speeds using eq. 1 and hence the relationship between speed and expected closure times (Fig. 4).

It is found that closure times actually declined at lower speeds. Furthermore, the ultimate minimization of the duration of an interaction occurs only if prey do not respond such that predators should further select lower speeds that reduce the chance of triggering a response. Thus, strike speeds in the range of 20–50 cm·s^{-1} should minimize the duration of interactions for the predators used in the present experiments (Fig. 4), similar to the speeds observed here in strikes by rainbow trout and smallmouth and rock bass. Therefore, all four predators are actually using the same general strategy of time minimizing in a strike. Differences occur because the low prey thresholds in response to the nonesocid fish necessitate opposite locomotor tactics compared with tiger musky.

Finally, these experiments show that rainbow trout and smallmouth and rock bass did not swim at the limits of their locomotor abilities. Therefore, in rainbow trout and smallmouth and rock bass, locomotor functional and morphology for BCF propulsion cannot be considered crucial factors modifying predator tactics as initially assumed in designing the experiments. Instead, prey response thresholds appear to be of greater importance.

Acknowledgments

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Orthophosphate Uptake Rate Constants are Mediated by the 10^3–10^4 Molecular Weight Fraction in Shield Lake Waters

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Although midsummer chlorophyll concentrations can be predicted from total phosphorus, attempts to identify all bioavailable phosphorus compounds has proven difficult. Inconsistencies in determining colloidal phosphorus utilization and the discovery that orthophosphate concentration and flux are poor predictors of lake trophic status has led us to postulate that other forms of phosphorus compounds, which may not be necessarily labeled over the radioisotopic uptake assay (^{32}P) period, are assimilated by natural phytoplankton assemblages. Using ultrafiltration methodology we test the hypothesis that the orthophosphate uptake rate constant can be physiologically varied upon changing the external concentration of selected molecular weight fractions in Shield lake waters. We determined that the fraction between molecular weight 10^3 and 10^4 significantly increased the orthophosphate uptake rate constant when exposed to the natural seston. Our discovery suggests that the orthophosphate uptake rate constant is subject to fluctuations depending on the availability of low molecular weight phosphorus metabolites in the external solution. The physiological basis of our observations may be a metabolic coupling between the activity of plasmalemma-bound phosphatases and the transport of PO_4^{3-} across the cell membrane.

Bien que la concentration de la chlorophylle estivale puisse être prédite à partir du phosphore total, l'identification des composés biodisponibles de phosphore demeure incertaine. D'une part la difficulté de définir l'utilisation du phosphore colloïdal par le seston, et d'autre part le fait que la concentration d'orthophosphate ou le flux ne sont pas capable de prédire le niveau trophique d'un lac, nous a mené à postuler l'existence d'autres formes de composés phosphorés qui, lors des mesures d'assimilation avec le radioisotope ^{32}P, pourraient être assimilées par le phytoplancton tout en demeurant exclues au traceur radioactif. Nous avons testé l'hypothèse que les vitesses d'assimilation de l'orthophosphate pouvaient être modifiées en changeant la concentration de ces composés phosphorés. Pour ce faire, nous avons utilisé l'ultrafiltration de façon à concentrer des fractions de différents poids moléculaire à partir des eaux du lac. Nous avons trouvé que des ajouts de fractions comprises entre 10^3 et 10^4 augmentaient de façon significative les vitesses d'assimilation du seston naturel. Ceci suggère que les vitesses d'assimilation observée dans les lacs du Bouclier pourraient être sujettes à des fluctuations reliées à l'utilisation par le phytoplancton de composés phosphorés à faible poids moléculaire. Nous croyons que ces observations sont liées au couplage entre les phosphatases situées sur la membrane cellulaire et le transport de l'orthophosphate à travers la membrane.

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Although midsummer chlorophyll *a* concentrations can be predicted from total phosphorus at spring overturn for a number of North American lakes (Dillon and Rigler 1974), it is not precisely known which phosphorus compounds are responsible for this relationship. The molecular size of phosphorus compounds and their fluxes between compartments were elucidated (Lean 1973a, 1973b), yet several aspects of the phosphorus cycle remain enigmatic. In New Zealand lakes, reactive high molecular weight phosphorus (RHMWP) was not consistently utilized and did not always result in biomass yields comparable with those obtained with PO_4 (Paerl and Downes 1978; White and Payne 1980). Incomplete utilization of RHMWP may occur presumably because the time scale of induction of phosphatases at typical laboratory cell division rates ($>1 \cdot d^{-1}$) may be considerably different from cells dividing at slower rates (<0.5–$1 \cdot d^{-1}$) in natural waters. Alternatively, the remaining phosphorus compounds may have been refractory to the seston.

In Canadian lakes, when extreme orthophosphate depletion occurs, diphasic kinetics in ^{32}P uptake is often observed. Under these conditions "colloidal P" is rapidly labeled (Lean and Nalewajko 1979), and this product is mostly unavailable to the seston (Lean 1973b). However, in long-term (7 d) limnocorral experiments carried out in Canadian Precambrian Shield lake waters, isotopic equilibrium was not achieved under either oligotrophic or eutrophic conditions (Levine and Schindler 1980), indicating that not all the relevant phosphorus compartments are labeled. It may be that differences in the rate of colloidal phosphorus labeling (and hence the time scale to isotopic equilibrium) are related to the presence of unlabeled phosphorus compounds available to the seston.

A recent intriguing discovery is that the orthophosphate concentration, as determined by the Rigler radiobioassay (Rigler 1966), was invariable during the ice-free season in two Shield lakes possessing a 3× difference in chlorophyll *a* concentrations (Levine 1976; Levine and Schindler 1980). On the basis of their results, these authors concluded that the PO_4^{3-} concentration was a poor predictor of lake trophic status. Furthermore, only the total dissolved phosphorus (TDP) was correlated with particulate phosphorus, suggesting that the main source of phosphorus is the TDP pool. This argument is supported by the well-known physiological temporal uncoupling between uptake and growth, especially when phytoplankton are phosphorus starved (Lean and Nalewajko 1976; Nalewajko and Lean 1978; Rhee 1973; Gotham and Rhee 1981), and the fact that when used in situ, the radiobioassay measures PO_4^{3-} flux on time scales (typically <1 h) that are considerably shorter than the time frame of phytoplankton and bacterial turnover rates (typically >24 h).

Consequently, the flux of PO_4 could reveal only a fraction of the complete flux of nutritionally important phosphorus compounds into the cell. A corollary of these arguments is that the PO_4^{3-} concentration may be a reflection of biological processes rather than a forcing variable. If we postulate that in addition to orthophosphate, phytoplankton also assimilate and hydrolyze low molecular weight phosphorous compounds, then modifying the external concentration of the latter should affect cellular phosphorus cycling. Therefore, we tested the hypothesis that the $^{32}PO_4^{3-}$ uptake rate constant may be mediated by low molecular weight solutes present in natural lake waters. We present series of experiments involving progressively more complex molecular weight fractionation of natural lake water. These fractions were exposed to the lake seston and the changes in the uptake slope were determined. Since these changes could also result from abiotic adsorption and complexing reactions, we examined these possibilities as well.

Materials and Methods

All experiments were carried out with water from lac Tantarie, an acidic and oligotrophic Shield lake located (47° 04′N, 71°33′W) 42 km north of Quebec City; limnological characteristics are summarized in Table 1. During our experiments the phytoplankton assemblage was dominated in August by the blue-greens, *Merismopedia tenuissima* and *Microcystis* sp., and in October by the chrysophytes, *Chrysococcus* sp. and *Chromulina* sp., Radiophosphorous uptake by seston was followed by its disappearance from the Millipore 0.45-μm filtrate. Since in most experiments, 200 mL of seston was spiked with 25 mL of a concentrated molecular weight fraction, experiment 1 was conducted to ascertain that in control experiments 25 mL of filtered lake water (FLW) could be replaced with 25 mL of deionized water from a Millipore Milli-Q3RO/Milli-Q2 deionizer. The $^{32}PO_4$ uptake of the intact assemblage was compared with that of the seston progressively diluted with varying proportions of 2:0, 1:1, and 0:2 filtered lake water: Millipore "Q" water. After spiking with $^{32}PO_4^{3-}$, 5-mL aliquots were filtered and rinsed with 10 mL of Millipore "Q" water containing 10 μg "cold" $^{31}PO_4^{3-} \cdot L^{-1}$. Filtrate radioactivity was detected by liquid scintillation (LKB rackbeta), using either Cerenkov counting (^{32}P) or emulsion counting (^{33}P) in Aquasol. Experiment 2 was designed to test whether two fractions (> 50 000 molecular weight cutoff (MWCO) and < 50 000 MWCO, respectively) might have an effect on the $^{32}PO_4$ uptake rate constant. The ultrafiltration methodology followed the recommendations of Buffle et al. (1978, 1982) and Buffle and Deladoey 1982). To avoid possible changes in labile phosphorus forms we used no supporting electrolyte. Lake water was collected on 3 August 1981; within 2 h, 800 mL was filtered through several 0.45-μm HAWP Millipore filters to avoid clogging (Fig. 1). The filtrate was subdivided into two 400-mL fractions; the first (T) was rotoevaporated (Büchi, Rotovapor-R) to a volume of 25 mL (16× concentration) and the second was passed through an Amicon thin-channel ultrafiltration assembly equipped with an XM50 filter. The > 50 000 MW fraction (I) was concentrated to 25 mL, and the 375-mL residue (< 50 000 MW fraction (II)) was rotoevaporated (30°C) to 25 mL. The three 16× (25 mL) concentrates were then added to separate 200-mL aliquots of fresh unfiltered lake water obtained on 6 August 1981; a fourth aliquot received 25 mL of Millipore "Q" water and served as control. Within 2 min, all four reactors were spiked with $^{33}PO_4^{3-}$ that had been immediately prefiltered through a 0.22-μm Millipore filter to remove any polymerized phosphates. Five-millilitre aliquots from each reactor were filtered at 0, 2, 4, 6, and 8 min and counted.

TABLE 1. Limnological characteristics of lac Tantarie.

Elevation (m)	500
Precipitation (cm)	145
Lake area (km^2)	1.33
Watershed area (km^2)	12.1
Maximum depth (m)	21.0
Conductivity ($\mu S \cdot cm^{-1}$)	18.0
pH	5.1
Alkalinity ($mg\ C \cdot L^{-1}$)	<0.2
Rainwater pH	4.2
Ca ($mg \cdot L^{-1}$)	1.5
Mg ($mg \cdot L^{-1}$)	0.2
K ($mg \cdot L^{-1}$)	0.3
Na ($mg \cdot L^{-1}$)	0.5
Fe ($mg \cdot L^{-1}$)	0.04
Mn ($mg \cdot L^{-1}$)	0.04
Al ($mg \cdot L^{-1}$)	0.22
Cl ($mg \cdot L^{-1}$)	0.3
SO_4 ($mg \cdot L^{-1}$)	5.7
$NO_3 + NO_2$ ($mg \cdot L^{-1}$)	0.53
Color (hazen units)	5.0
Chl *a* ($\mu g \cdot L^{-1}$)	0.2–2

The operational procedure of experiment 3 was similar to experiment 2 except that the lake water (13 August 1981) was filtered through a 0.2-μm Nuclepore filter and molecular weight fractionation was carried out on XM100 and PM10 Amicon filters (Fig. 1). As before, excluded organic matter was directly concentrated at the filter interfaces, whereas the filtrates were rotoevaporated (35°C).

Four fractions were thus obtained: organic matter (OM) > 10^5 MW (I, filter concentrate), 10^5 MW > OM > 10^4 MW (II, rotoevaporated), OM > 10^4 MW (III, filter concentrate), and OM < 10^4 MW (IV, rotoevaporated). An aliquot of the 0.4-μm Nuclepore filtrate was also rotoevaporated to 25 mL (T). According to this fractionation scheme, the orthophosphate concentrations, assuming no loss to the filtration assembly, should be equal to the lake water in fractions I and III and should be concentrated 16× in fractions T, II, and IV. We added the concentrates to 200 mL of unfiltered lake water obtained on 14 August 1981 and proceeded as in experiment 2. Experiment 4 was identical to experiment 3 except that fraction IV was further fractionated using an Amicon stirred-cell assembly and a UMO5 filter to yield 10^4 > OM > 5×10^2 (V, filter concentrated) and OM < 5×10^2 (VI, rotoevaporated).

Experiment 5 was carried out to verify if over a period of 30

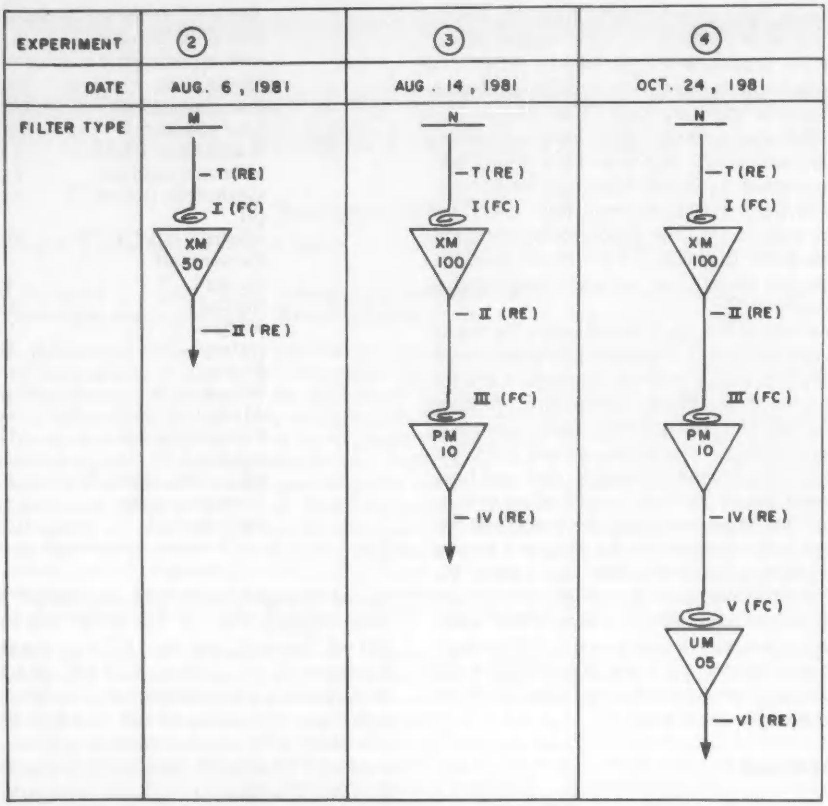

FIG. 1. Fractionation scheme utilized in experiments 2, 3, and 4. M = Millipore, 0.45 μm; N = Nuclepore, 0.2 μm; ∇ = ultrafilters with Amicon designations; I–IV, fractions; RE, rotoevaporated; FC, filter concentrate. All fractions were concentrated 16×.

min there was abiotic fixation of $^{32}PO_4^{3-}$ into colloidal size phosphorus compounds. Lake water (16 mL) obtained on 18 August was filtered through a 0.4-μm Nuclepore filter and subdivided into two (8 mL) treatments, with and without 1% formaldehyde. Filtered (0.22-μm Millipore) radiophosphorus was added, and following a 30-min incubation each 8-mL aliquot was subdivided into a 2-mL fraction for total radioactivity, a 2-mL fraction for Sephadex separation, and a 2-mL fraction that was refiltered on a 0.45-μm Millipore filter to obtain any filter-retainable ^{32}P-labeled compounds. The Sephadex separation was accomplished in specially constructed centrifuge tubes (P. Brassard and J. C. Auclair, unpublished) packed with Sephadex G-25 beads. Elution was accomplished by spinning and stopping at 1-min intervals and adding 1 mL of eluant (0.3% NaCl, 0.02% NaN_3). Although this procedure can only separate colloidal from orthophosphate, it allows the simultaneous separation of four samples within 30 min, a considerable gain over column Sephadex fractionation techniques (30–40 min·sample^{-1}). The radioactivity of the three 2-mL fractions was then assayed. Experiment 6 was designed to test for $^{32}PO_4^{3-}$ abiotic fixation in the presence of fraction V at 2.5× the ambiant lake concentration. Two lakewater (45 mL) aliquots were placed in separate polycarbonate beakers and reactor No. 1 was spiked with 2.5 mL of formaldehyde. Both reactors were then spiked with 5 mL of fraction V, followed by $^{32}PO_4^{3-}$ that had been previously filtered through a 0.22-μm Millipore filter to remove polyphosphates. Subsamples (5 mL) were then withdrawn, filtered (0.45-μm Millipore), and rinsed at 0, 2, 4, 6, and 8 min, as described above.

Results and Discussion

Assuming that there was no new synthesis of membrane transport sites in the assemblage during the assay period, we needed to ascertain that the uptake constants obtained from the assays reflected the activity of the overall phosphorus transport mechanism of the assemblage, specifically that cellular release of labeled colloidal phosphorus or labeled orthophosphate did not significantly alter the slope of the uptake curve during the 10-min assay interval. These initial assumptions are implicit every time a log-linear curve is expected from ^{32}P bioassays. Experiment 5 shows that the abiotic fixation of the label was not a problem during the uptake (see following). In addition, we have demonstrated that log-linearity is inconsistent with a significant adsorption of label to/by a filter-retainable compound (see Appendix).

In experiment 1, the $^{32}PO_4^{3-}$ uptake kinetics of lake water diluted with either filtered lake water or Millipore "Q" were identical (Fig. 2). Had the filtered lake water contained significantly more orthophosphate than the Millipore "Q" water,

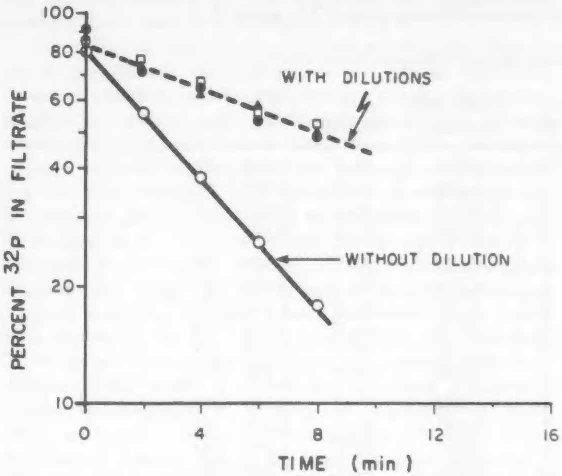

FIG. 2. Results of experiment 1: testing the reliability of the control. Four reactors containing various mixtures of unfiltered lake water, filtered lake water, and Millipore "Q" water were tested for $^{32}\mathrm{PO}_4^{3-}$ uptake. Dilution table:

Symbol	Lake water (mL)	Filtered lake water (mL)	Millipore "Q" water (mL)
●	100	200	0
□	100	100	100
▲	100	0	200
○	300	0	0

one would have expected a further decrease in the slope of the filtered lake water $^{32}\mathrm{PO}_4^{3-}$ uptake assay. This shows that "Q" water could be used as a control because it had no effects on the $^{32}\mathrm{PO}_4^{3-}$ pool. In addition, the difference in uptake rate between the diluted and the undiluted samples was entirely due to the dilution of the lake water, since the ratio of the uptake constants matched the dilution ratio of 1 part lake water to 2 parts filtered lake water or "Q" water.

Thus, in our Millipore water controls, the uptake rate constant should be an exponentially decreasing function with time, dependant uniquely on the number of cellular transport sites and the initial concentration of $^{31}\mathrm{PO}_4^{3-}$. Between our experimental 225-mL lake water aliquots and our controls, an increase in the uptake rate can be attributed to isotope concentration (through a decrease in the $^{31}\mathrm{PO}_4^{3-}$-pool) or enhanced uptake (as a consequence of the added concentrates), while a decrease can be attributed to isotope dilution (increase in the $^{31}\mathrm{PO}_4^{3-}$- pool) or uptake inhibition (Fig. 3).

In experiment 2, three concentrated fractions, T, I, and II, added to unfiltered lake water were compared with lake water + Millipore "Q" controls (C) (Table 2). In the presence of the T fraction, the uptake rate constant was significantly reduced, while both fractions I and II increased the uptake rate constant relative to the Millipore "Q" control (C). The reduced uptake rate with the 0.45-μm Millipore filtered and rotoevaporated lake water was expected because this treatment concentrates the $^{31}\mathrm{PO}_4^{3-}$ pool, thus diluting the $^{32}\mathrm{PO}_4^{3-}$ tracer. However, the uptake rate constants obtained with fractions I and II were surprising, especially since fraction II should have had a nonlabeled orthophosphate concentration similar to fraction T.

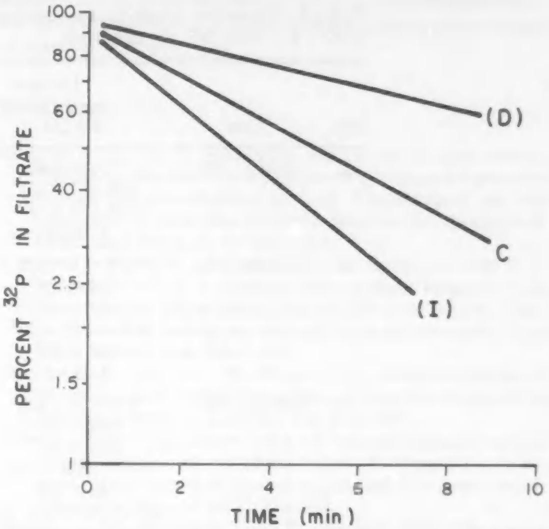

FIG. 3. Rationale used for interpreting ^{32}P uptake curves. The slope C is obtained from control experiments in which an equal volume of Millipore "Q" water was substituted for the volume of concentrate. Deviations from C are represented by curves D and I. Curve D can occur through isotope dilution (increase in the $^{31}\mathrm{PO}_4^{3-}$ pool) or uptake inhibition. Curve I is a consequence of isotope concentration (decrease in the $^{31}\mathrm{PO}_4^{3-}$ pool) or enhancement of uptake.

At this point, it could be argued that polyhydroxocomplexes of iron or aluminium clogged in/on the filter matrix adsorbing orthophosphate during the ultrafiltration process reducing the PO_4^{3-} in the concentrates and consequently the uptake rate constant would simply be a reflection of the increased $^{32}\mathrm{PO}_4^{3-}$ specific activity. Alternatively, $^{31}\mathrm{PO}_4^{3-}$ could be bound abiotically upon the immediate addition of concentrates, containing compounds with surface-active properties, to the lake water (although kinetic arguments mediating such a rapid transfer are hard to imagine). Both of these considerations were examined in later experiments and discussed subsequently.

In experiment 3 (Table 2), variations in the uptake rate constants with fractions T and II were similar to experiment 2 whereas fractions I and III were not significantly different from the two controls. This observation refutes the theory of increased adsorption during ultrafiltration. Since the contact time during concentration of fractions I and III at the filter interface is far longer than that of fractions II and IV, which flow through and are then concentrated by rotoevaporation, one would expect a greater loss of $^{31}\mathrm{PO}_4^{3-}$ from fractions I and III and subsequently a greater uptake rate constant. Since this was not observed in experiments 3 and 4 (see following), one may conclude that there was a negligible adsorption of $^{31}\mathrm{PO}_4^{3-}$ in the membrane matrix.

Given that the operational procedure was identical when concentrating fractions T, II, and IV, the $^{31}\mathrm{PO}_4^{3-}$ pool should have been equally concentrated, and one might have expected similar uptake curves when unfiltered lake water was exposed to these fractions. Since this was not observed, we postulated that nonlabeled compounds in fraction II and possibly IV were modulating the uptake rate constant. This prompted us to carry out a third separation to study more carefully the behavior of $10^4 < \mathrm{OM} < 500$ MW (V) and $\mathrm{OM} < 500$ MW (VI) fractions.

TABLE 2. Molecular weight fractions and log-linear parameters for experiments 2, 3, and 4. $^{*}P < 0.05$; $^{**}P < 0.01$; NS, not significant.

Exp.	Date	Fraction MWCO	Fraction No.	Uptake rate constants	Intercept	r^2	t
2	6 Aug. 1981	$< 0.45\ \mu m$	T	0.065	96.3	0.963	**
		$OM > 5 \times 10^4$	I	0.166	92.9	0.997	**
		$OM < 5 \times 10^4$	II	0.165	86.3	0.994	*
		Control	C	0.125	91.6	0.995	—
3	14 Aug. 1981	$OM < 0.4\ \mu m$	T	0.022	96.5	0.979	**
		$OM > 10^5$	I	0.169	92.2	0.998	NS
		$OM < 10^5$	II	0.227	85.8	0.993	**
		$10^4 < OM < 10^5$	III	0.175	91.3	0.994	NS
		$OM < 10^4$	IV	0.133	90.3	0.999	NS
		Control	C	0.150	85.4	0.996	—
4	24 Oct. 1981	$OM < 0.2\ \mu m$	T	0.023	97.8	0.867	**
		$OM > 10^5$	I	0.067	94.3	0.999	NS
		$OM < 10^5$	II	0.069	95.0	0.994	NS
		$10^4 < OM < 10^5$	III	0.077	97.8	0.997	NS
		$OM < 10^4$	IV	0.072	97.3	0.997	NS
		$10^4 < OM < 5 \times 10^2$	V	0.102	99.9	0.994	**
		$OM < 5 \times 10^2$	VI	0.075	97.0	0.996	NS
		Control	C	0.068	95.04	0.991	—
				0.066	95.9	0.992	—

The uptake rate constants (Table 2) followed a similar trend to those in experiment 3. The 0.2-μm Nuclepore filtered and rotoevaporated fraction (T) had the most reduced uptake confirming the earlier results. The effect of fractions I, II, III, IV, and VI were not significantly different from the effect of the Millipore "Q water controls. An increase in the uptake rate constant was observed in the presence of fraction V.

The results of experiment 5 confirmed that both in the presence and absence of 1% formaldehyde, the recovery of orthophosphate in the Sephadex centrifugation procedure was greater than 95%. Therefore, the abiotic formation of colloidal phosphorus can be excluded. An identical experiment carried out with a preliminary filtration on 0.45-μm Millipore filters gave identical results, suggesting that in lac Tantarie, bacterial biomass can be as efficiently excluded on 0.4-μm Nuclepore as on 0.45-μm Millipore filters. In experiment 6, upon filtration in the presence of fraction V, the amount of retained radiolabel at each filtration interval was 15.4 ± 1.28% for the control and 14.4 ± 1.8% for the reactor treated with formaldehyde. This initial retention could be interpreted as an instantaneous adsorption of the radiolabel by fraction V. This is unlikely, however, since a similar retention in the absence of fraction V was observed with the assays in experiment 1 (Fig. 2) where the intercepts at $t = 0$ ranged from 80 to 85%. In addition, the intercepts observed with fractions II of experiment 3 and V of experiment 4 were the same as their respective controls. In these, an instantaneous adsorption of the label by the added concentrate would have yielded a decreased intercept and a lower coefficient of determination (Appendix). Therefore, the intercept of experiment 6 was caused by membrane retention.

Since in experiments 5 and 6, we were unable to prove abiotic colloidal phosphorus formation, it follows that the variations in the uptake rate constants were not due to the adsorption of PO_4^{3-} on iron hydroxides or compounds with surface-active properties such as mixed complexes of fulvic acids–metal phosphate of Al(III) and Fe(III). Rather, the observed increases in the uptake rate constant must reflect a true enhancement of PO_4^{3-} uptake. Physiologically, enhancement of uptake could occur if the transport of $^{32}PO_4^{3-}$ and $^{31}PO_4^{3-}$ were metabolically coupled to the activity of plasmalemma (cell space) bound phosphatases; the localization of phosphatases in the cell space (between the plasmalemma and the cell coat) has been confirmed in bacteria (Cheng et al. 1970; MacAlister et al. 1977) and the chlorophyte *Chlamydomonas reinhardi* (Matagne et al. 1976). Thus, any increase in extracellular substrate concentration (phosphomonoesters, nucleotide di-monophosphates) might result in enhanced uptake of radiophosphorus. Assays carried out in lac Tantarie during the following year showed very high activities in agreement with phosphatase activities in other acidic lakes (Jansson 1981; Jansson et al. 1981).

The mechanism for this enhanced uptake could also result from a requirement of phosphorus for the transport of a carbon source across the membrane. Lean and White (1983) showed that when the supply of phosphorus is low the uptake of orthophosphate by bacteria and microalgae predominates over larger phytoplankton. The uptake of several sugars by bacteria is known to be mediated by the phosphotransferase system (Saier 1982; Kaback 1970), so that it is possible that an increase in demand for orthophosphate occurs when a carbon source is transported. However, in Chesapeake Bay estuarine waters, Taft et al. (1977) showed, using a double-labeling technique, that glucose-6-phosphate was transported separately as glucose and phosphorus.

The carbon moiety was transported very slowly compared with the phosphate, suggesting that glucose phosphate had been split by phosphatases before assimilation and subsequent transport. The cleaved orthophosphate could thus regenerate phosphoenolpyruvate required to transport glucose. This dual transport system could be ecologically advantageous; if the phosphorus compound consists of a refractory organic moiety, then the preliminary hydrolysis by phosphatase would recover the phosphate group. In addition, if the organic part is metabolically needed then the hydrolysis step delivers both moieties to the individual transport systems.

The ecological importance of this enhanced uptake depends on its phosphorus contribution to cell growth processes. Although nonlinear relationships between surplus phosphorus, phosphatase activity, and steady-state growth rate are well known (Fitzgerald and Nelson 1966; Rhee 1973), the role of induced transients in phosphorus nutrition such as we observed has not been described as a function of phytoplankton cell division rates. Multiphasic uptake mechanisms occur in bacteria (Rosenberg et al. 1977) and fungi (Beever and Burns 1977; Burns and Beever 1979) over large changes in orthophosphate concentration, suggesting that an array of phosphorus transport systems possessing different kinetic properties can be assembled depending on the extracellular PO_4^{3-} concentrations. However, at environmental concentrations, several studies have confirmed that uptake is monophasic in culture experiments (Tilman and Kilham 1976; Nyholm 1977; Chisholm and Stross 1976) and marine systems (Perry and Eppley 1981; Perry 1976). In contrast, diphasic uptake has been frequently observed in Shield lake waters (Chamberlain 1968; Lean 1973b; Levine and Schindler 1980). The discrepancy in uptake kinetics may be due to differences in cell membrane architecture between laboratory-grown and natural phytoplankton populations. Since the cell membrane kinetically controls the flux of compounds to the intracellular medium, it would not be surprising to discover that the carrier systems are kinetically coupled to the rates of dissolution of biologically important compounds governed by the external solution chemistry. Thus, cells growing under steady-state conditions in simple inorganic culture media might possess a less complex membrane architecture than phytoplankton facing an assortment of potentially competing chemical reactions occurring in the natural aquatic system.

Our experiments demonstrate that in nature, transients in the orthophosphate uptake rate constant could occur as cells are exposed to rain event or wind-induced pulses of littoral zone allochtonous organic matter (Stewart and Wetzel 1981). The physiological basis underlying the transients in uptake should be pursued in further investigations, as the mechanism may have evolved to maintain constancy in rates of cell division (cf. Harris 1980). The variations in uptake rate detract from the value of using the rate constants as ecological state variables for interlake comparisons.

Finally, given that our study demonstrates that the orthophosphate uptake rate constant may be dependent on the availability and presence of low molecular weight metabolites, it is desirable to know their importance in maintaining the apparent constancy of orthophosphate concentrations in lakes of different trophic status (Levine and Schindler 1980). The relationship of these metabolites to the internal phosphorus pools should be examined. The effects they they produce in the short and long term upon surplus phosphorus or phosphatase activities are important in enhancing our understanding of interlake differences of phosphorus utilization per unit chlorophyll (Kalff and Knoechel 1978). In this context, phytoplankton growth rate should be examined as a function of internal phosphorus pools using more dynamic systems such as community continuous cultures (Smith and Kalff 1981; DeNoyelles et al. 1980, Barlow et al. 1973a, 1973b).

Acknowledgments

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Appendix

$^{32}PO_4{}^{3-}$ Filter Retention, Excretion of Labeled Phosphorus Compounds, and ^{32}P Uptake Curves

In his earlier work, Lean (1973b) dealt with the problem of the filtration artifact. After an initial incubation with $^{32}PO_4{}^{3-}$, he found that as much as 46% of the label in the filtrate was adsorbed upon refiltration on another Millipore membrane.

Two possibilities can explain this artifact: the label could be adsorbed by the membrane matrix, acting as a simple ion exchanger, or the orthophosphate label could be adsorbed by a filter-retainable compound, depending on the amount of the compound and its affinity for PO_4 at the time of filtration. In the first case, the amount adsorbed would be proportional to the concentration of the tracer left in solution at the time of filtration. In the second case, the normal uptake of phosphorus by the algal assemblage would be traced only by that portion of the label not initially adsorbed.

Of particular concern is how this adsorption affects the typical log-linear relationship that determines the orthophosphate uptake rate constant shown in Fig. 2. The simple sink-source model predicts

$$(1)\qquad C = C_0 e^{-kt}$$

where C = amount of tracer at t and C_0 = amount of tracer at t = 0.
A log transformation yields

$$(2)\qquad \ln C = \ln C_0 - kt$$

which is a linear relationship having a slope of $-k$.

We first examine the situation in which the filter adsorption (f) is proportional to the amount of tracer remaining in solution at each filtration interval. The quantity of remaining tracer is described by

$$(3)\qquad C = (1 - f)\, C_0 e^{-kt}$$

where f represents the fraction of tracer adsorbed on the filter.
A log transformation of equation 3 yields

$$(4)\qquad \ln C = \ln [(1 - f)\, C_0{}^{-kt}]$$
$$= [\ln C_0 - \ln f] - kt$$

resulting in a slope identical to equation 2 and a decreased intercept.
Second, if there is a loss of tracer at time zero, then uptake proceeds with the remaining tracer according to

$$(5)\qquad C = [(C_0 - A_0)e^{-kt} - A_0]$$

where A_0 represents the proportion of tracer lost at time zero.
Now, including our filter (f), we have

$$(6)\qquad C = (1 - f)\, [(C_0 - A_0)e^{-kt} - A_0].$$

A log transformation performed on equation 6 results in

$$(7)\qquad \ln C = -\ln f + \ln [(C_0 - A_0)e^{-kt} - A_0]$$

and since the log transformation of a sum cannot be resolved into individual terms, a differentiation is needed to obtain the slope:

$$\text{(8)} \quad \text{slope} = \frac{d(\ln C)}{dt} = -k\left[\frac{(C_0 - A_0)e^{-kt}}{(C_0 - A_0)e^{-kt} - A_0}\right].$$

Thus, depending on the magnitude of A_0, the relationship departs from log-linearity. When $A_0 = 0$, equation 6 yields a value of $-k$.

Our demonstration implies that log-linearity and an initial adsorption of tracer at time 0 are mutually exclusive hypotheses. Thus, if filter retention is proportional to remaining tracer at various filtration times, the estimate of the slope ($-k$) should be unbiased. If filter retention is not proportional to remaining isotopic activity, one would expect significant deviations from log-linearity.

Associations among Chironomidae and Sandy Substrates in Nearshore Lake Michigan[1]

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Winnell, M. H., and D. J. Jude. 1984. Associations among Chironomidae and sandy substrates in nearshore Lake Michigan. Can. J. Fish. Aquat. Sci. 41: 174–179.

Chironomids and sediments were collected at 3- to 15-m depths along the shoreline of eastern Lake Michigan from 1978 to 1980. Chironomids were the most frequently occurring (92% of samples), most diverse (41 taxa), and the second-most numerous ($1634 \cdot m^{-2}$) group in this depth regime. The generalized sediment type was moderately sorted, fine sand. Sediments were grouped into three categories roughly corresponding to coarse ($<2\phi$), fine (2–3ϕ), and very fine ($\geq 3\phi$) sands. Nonparametric tests and a comparison of frequency distributions and densities distinguished chironomid–substrate associations. Two species were strongly associated with coarse sand, 5 species with coarse–fine sands and fine–very fine sands, and 11 species with very fine sand. We postulate that observed chironomid–substrate associations were related in part to morphological differences among taxa. Species most strongly associated with coarse sediments were small, slender, and fast-moving forms with tough outer body integuments, morphological characteristics that are necessary for survival in the ephemeral, physically controlled environment. In the more stable, predictable environment where fine and very fine sands were most evident, species exhibited a wider variety of morphological characteristics, which included soft-bodied, tubicolous forms.

De 1978 à 1980, les auteurs ont recueilli des échantillons de sédiments et de chironomidés dans la partie est du lac Michigan, à des profondeurs variant de 3 à 15 m. Les chironomidés constituaient le groupe le plus fréquemment présent (92% des échantillons), le plus varié (41 taxons et le second en abondance ($1634 \cdot m^{-2}$). Le type généralisé de sédiment était le sable fin modérément trié. Les sédiments ont été classés en trois groupes, correspondant à peu près au sable grossier ($<2\phi$), fin (2 à 3ϕ) et très fin ($\geq 3\phi$). À l'aide de tests non paramétriques et d'une comparaison des distributions des fréquences et des densités, on a séparé les associations entre les chironomidés et les substrats. Ainsi, 2 espèces étaient étroitement associées au sable grossier, 5 autres, au sable variant de grossier à fin tandis que 11 autres peuplaient le sable très fin. Les auteurs formulent l'hypothèse que les associations observées entre les chironomidés et les substrats sont reliées en partie aux différences morphologiques entre les taxons. Les espèces retrouvées le plus souvent dans les sédiments grossiers sont de petites formes minces et rapides, aux téguments externes durs — caractéristiques nécessaires à la survie dans un environnement éphémère et influencé par les facteurs physiques. Dans l'environnement plus stable où abonde le sable fin et très fin, les espèces montraient une plus grande variété de caractères morphologiques, dont des formes tubicoles à corps mou.

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The association between substrate grain size and the distribution of chironomids in the Great Lakes has not been adequately studied. Most benthic surveys in the Great Lakes have considered depths and consequently substrates over a wide range, resulting in variable conclusions. Chironomids preferred sandy or silty sands over finer or coarser sediment at 0–20 m and sandy silt at 21–40 m in Lake Michigan (Alley and Mozley 1975). Weak associations between chironomids and percent sand were observed in Lake Superior (Dermott 1978). However, chironomids in Lake Ontario showed no significant sediment preferences (Nalepa and Thomas 1976). Still other investigators have inferred association through substrate–depth–chironomid co-occurrences (Kinney 1972; Mozley and Garcia 1972; Mozley and Winnell 1975; Geers 1977).

Wave activity is the dominant force controlling substrate distribution at depths less than 8 m along the shoreline of Lake Michigan (Mozley and Garcia 1972). Storm activity influences the distribution of sediments at depths greater than 8 m, and alongshore currents produce rippling of sediments to a depth of 12 m (Mozley and Garcia 1972). Wave current activities in our survey area produce a sediment that is nearly always 95–98% sand (Winnell and Jude 1979, 1980, 1981). We examined the relationship between the abundance and distribution of chironomids among these sandy sediments occurring in the nearshore environment of Lake Michigan.

Methods

Benthic macroinvertebrates and sediments were collected during April, July, and October from 1978 to 1980 near the J. H. Campbell Power Plant, eastern Lake Michigan (42°53′N, 86°13′W). Sixty triplex Ponar (see Mozley and Chapelsky

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1973) grab samples were collected each month from the University of Michigan's R/V *Mysis*. Sample sites were located at 3-, 6-, 9-, 12-, and 15-m depths along each of two transects situated 0.16 and 5.0 km north of the plant. Six replicates were collected at each site per month, and 540 samples were collected from the survey area.

The sample from one side chamber of the Ponar grab was used to estimate benthic density and diversity. Benthic invertebrates were concentrated from debris using a 0.2-mm mesh net and stored in 4% buffered formaldehyde solution. Approximately 30 g of the remaining portion of each Ponar grab sample was retained to estimate sediment type. Sediment samples were mechanically sieved and analyzed for moment measure statistics and percent weight per grain size unit (ϕ) (Krumbein 1938; Seibel et al. 1974).

From the range of grain size categories observed, three groups of grain size were established that roughly corresponded to coarse sand ($<2\phi$), fine sand ($2-3\phi$), and very fine sand ($\geqslant 3\phi$). The Mann–Whitney *U*-test and the median test (Siegel 1956; Elliott 1971) were used to determine if the distributions of samples with (presence) and without (absence) individuals for each species were significantly different among the three sands. Both tests determined whether the two sets of samples were drawn from a common population with similar distributions (nonsignificance) or from populations with dissimilar distributions (significance) at $\alpha = 0.05$. In particular, the median test determined whether samples with and without a given species had distributions similar or dissimilar to the median value for the three sands. Frequency distributions and average abundance were determined for samples with and without a given species above and below the median value for each sand.

Results

Chironomidae were the most frequently occurring (92% of samples), the most diverse (41 species) (Table 1), and the second-most numerous ($1634 \cdot m^{-2}$) macrobenthic group in the survey area. The five most numerous chironomid taxa were *Saetheria* cf. *tylus*, *Paracladopelma camptolabis*-gr., *Robackia* cf. *demeijerei*, *Psectrocladius* cf. *simulans*, and *Chironomus fluviatilis*-gr. (Table 2). Most numerous at the shallowest depths were *R*. cf. *demeijerei* and *P*. cf. *simulans*. Most abundant species at mid-depths were *C. fluviatilis*-gr., *P. camptolabis*-gr., and *P*. cf. *scalaenum*. At the deepest depths, *Hydrobaenus* cf. *pilipes* and *Heterotrissocladius* cf. *changi* were most numerous. Regardless of depth, *S*. cf. *tylus* was very abundant and among the five most numerous species. Generally, total chironomid densities were similar across all depths.

The general sediment type from 3 to 15 m was moderately sorted, fine sand. Grain sizes ranged from gravel (-3 to -2ϕ) to clay ($9-10\phi$). The primary sedimentary components were medium sand ($1-2\phi = 19\%$ of total sample weight (hereafter, total sample weight will be implied)), fine sand ($2-3\phi = 58\%$), and very fine sand ($3-4\phi = 16\%$) (Table 3). When combining the coarsest grain sizes $<2\phi$ (hereafter called coarse sand), this fraction of the sediment averaged 25% of the total, with a median value of 15%. Similarly, when combining the finest grain sizes $\geqslant 3\phi$ (hereafter called very fine sand), this portion averaged 17% of the total, with a median value of 11%. The average and median value for the $2-3\phi$ fraction (fine sand) was 58% for each. The percent composition of the average substrate type attributable to the very fine-sand fraction increased with increasing depth. The coarse-sand fraction decreased from 3 to 9 m and then increased at 12 and 15 m. The fine-sand fraction was greatest at 9 and 12 m.

TABLE 1. Chironomidae collected from 1978 to 1980 at 3–15 m near the J. H. Campbell Plant, eastern Lake Michigan.

Taxon
Chironomidae
Chironominae
Chironomini
Chironomus anthracinus-gr.
Chironomus fluviatilis-gr.
Chironomus halophilus-gr.
Cladopelma sp.
Cryptochironomus cf. *rolli*
Cryptochironomus sp. 1
Cryptochironomus sp. 2
Cryptochironomus sp. 3
g. nr. *Cyphomella*
Endochironomus sp.
Glyptotendipes sp.
Parachironomus cf. *abortivus*
Parachironomus sp. 1
Paracladopelma cf. *nereis*
Paracladopelma cf. *undine*
Paracladopelma cf. *winnelli*
Phaenopsectra sp.
Polypedilum cf. *scalaenum*
Polypedilum cf. *simulans/digitifer*
Polypedilum cf. *tuberculum*
Polypedilum sp. 2
Robackia cf. *demeijerei*
Saetheria cf. *tylus*
Tanytarsini
Cladotanytarsus sp.
Micropsectra sp.
Tanytarsus sp.
Orthocladiinae
Cricotopus (*Cricotopus*) *tremulus*-gr.
Cricotopus (*Cricotopus*) sp.
Cricotopus (*Isocladius*) *sylvestris*-gr.
Heterotrissocladius cf. *changi*
Heterotrissocladius cf. *oliveri*
Hydrobaenus cf. *pilipes*
Nanocladius sp.
Orthocladius (*Euorthocladius*) sp.
Orthocladius (*Orthocladius*) sp. *obumbratus*
Paracladius sp.
Psectrocladius cf. *simulans*
Thienemanniella sp.
Diamesinae
Potthastia cf. *longimanus*
Prodiamesinae
Monodiamesa cf. *tuberculata*
Tanypodinae
Procladius sp.

Results of the Mann–Whitney and median tests distinguished three generalized chironomid–sediment associations (Table 4). Two species were strongly associated with coarse sand. Five chironomid species were associated with either coarse–fine sands or fine–very fine sands. Eleven species were strongly associated with very fine sand.

Cryptochironomus sp. 1 and *R*. cf. *demeijerei* occurred explicitly in the coarser sediment types. Frequency of occur-

TABLE 2. Mean density (No. · m^{-2}) for chironomid species at 3-m depth intervals ($N = 108$) and over all depths ($N = 540$).

Taxon	Depth (m) 3	6	9	12	15	3–15
Chironomus fluviatilis-gr.	115	210	302	76	16	144
Cladotanytarsus sp.	1	28	196	58	7	58
Cryptochironomus cf. *rolli*	53	18	19	13	3	21
Cryptochironomus sp. 1	53	14	1	1	0	14
Cryptochironomus sp. 2	24	59	154	113	48	80
Cryptochironomus sp. 3	10	8	12	0	1	6
Heterotrissocladius cf. *changi*	0	5	14	52	54	25
Hydrobaenus cf. *pilipes*	1	2	5	37	106	30
Micropsectra sp.	0	1	10	84	34	26
Monodiamesa cf. *tuberculata*	1	3	19	33	90	29
Orthocladius cf. *obumbratus*	18	7	79	43	6	30
Paracladopelma camptolabis-gr.	65	220	483	260	116	229
Paracladopelma cf. *winnelli*	2	7	19	11	17	11
Polypedilum cf. *scalaenum*	5	35	324	227	74	133
Polypedilum cf. *tuberculum*	0	1	6	19	72	18
Psectrocladius cf. *simulans*	656	21	31	18	1	145
Robackia cf. *demeijerei*	497	249	95	44	27	182
Saetheria cf. *tylus*	405	729	171	314	315	387
Total Chironomidae	1978	1720	1982	1481	1006	1634

TABLE 3. Average percentage of total weight for grain size categories (ϕ) occurring at 3-m depth intervals ($N = 108$) and over all depths ($N = 540$) (SD = sorting coefficient).

Substrate ϕ	Depth (m) 3	6	9	12	15	3–15
< −3	0.0	0.1	0.0	0.0	<0.1	<0.1
−3 to −2	<0.1	0.2	0.1	<0.1	<0.1	0.1
−2 to −1	0.1	0.9	0.1	0.2	0.1	0.3
−1–0	0.4	3.0	0.3	0.5	0.8	1.0
0–1	2.6	10.5	1.5	2.5	4.0	4.2
1–2	38.6	16.5	7.8	12.4	21.0	19.3
2–3	49.8	59.1	70.4	61.7	47.0	57.6
3–4	7.5	7.9	18.3	21.9	26.1	16.3
4–5	0.8	0.8	0.7	0.6	0.5	0.7
5–6	0.0	0.2	0.1	0.0	<0.1	0.1
6–7	0.0	<0.1	<0.1	0.0	<0.1	<0.1
7–8	0.0	0.1	<0.1	0.0	<0.1	<0.1
8–9	0.0	<0.1	<0.1	0.0	<0.1	<0.1
≥9	0.0	0.4	0.5	0.0	0.2	0.2
Mean	2.12	2.08	2.56	2.52	2.44	2.34
SD	0.58	0.68	0.52	0.62	0.73	0.63
<2 (= coarse sand)	41.6	31.2	9.7	15.6	26.0	24.8
2–3 (= fine said)	49.8	59.1	70.4	61.7	47.0	57.6
≥3 (= very fine sand)	8.3	9.5	19.6	22.5	26.8	17.3

rence and density were greatest in substrates when the coarse component exceeded 15% and the very fine component was <11% (Table 5). While it was evident that both taxa were strongly dependent on coarser substrates, presence–absence tests for *Cryptochironomus* sp. 1 were not significant for the fine-sand component, whereas those for *R.* cf. *demeijerei* were significant. This trend suggested that the former taxon may be more strongly associated with coarse substrates than the latter.

Species occurring in strong conjunction with coarse–fine sands were *S.* cf. *tylus*, *P.* cf. *simulans*, *Cryptochironomus* cf. *rolli*, and *Cryptochironomus* sp. 3. In general, these taxa were collected from substrates in which coarse sand was >15% and very fine sand was <11% of the total. While somewhat similar to the previous two species, occurrences of these four species indicated increased reliance on fine sand (Table 5).

A single species, *C. fluviatilis*-gr., was strongly associated

TABLE 4. Attained levels of significance for each chironomid species in the $<2\phi$, $2–3\phi$, and $\geq 3\phi$ sediment categories ($N = 540$ for each test). Each test compares the distribution of samples with and without chironomids of a particular taxon in each sediment category (*significant at $\alpha = 0.05$).

	$<2\phi$		$2–3\phi$		$\geq 3\phi$	
Taxon	Mann–Whitney *U*-test	Median test	Mann–Whitney *U*-test	Median test	Mann–Whitney *U*-test	Median test
Chironomus fluviatilis-gr.	0.0000*	0.0000*	0.0002*	0.0000*	0.0848	0.3653
Cladotanytarsus sp.	0.0000*	0.0000*	0.0000*	0.0000*	0.0001*	0.0000*
Cryptochironomus cf. *rolli*	0.3051	0.0856	0.0273*	0.0551	0.4822	0.2471
Cryptochironomus sp. 1	0.0000*	0.0000*	0.1302	0.1249	0.0000*	0.0001*
Cryptochironomus sp. 2	0.0000*	0.0000*	0.0010*	0.0098*	0.0000*	0.0000*
Cryptochironomus sp. 3	0.3764	0.1752	0.3449	0.3779	0.1851	0.0593
Heterotrissocladius cf. *changi*	0.0631	0.0610	0.0021*	0.0004*	0.0000*	0.0000*
Hydrobaenus cf. *pilipes*	0.6705	0.3582	0.0065*	0.0025*	0.0000*	0.0000*
Micropsectra sp.	0.9331	0.4388	0.0503	0.1402	0.0156	0.0220*
Monodiamesa cf. *tuberculata*	0.0337*	0.0841	0.0001*	0.0000*	0.0000*	0.0000*
Orthocladius cf. *obumbratus*	0.0001*	0.0022*	0.0022*	0.0338*	0.0211*	0.0211*
Paracladopelma camptolabis-gr.	0.0000*	0.0000*	0.0000*	0.0000*	0.0000*	0.0003*
Paracladopelma cf. *winnelli*	0.0030*	0.0072*	0.7141	0.1116	0.0000*	0.0016*
Polypedilum cf. *scalaenum*	0.0000*	0.0000*	0.0823	0.2174	0.0000*	0.0000*
Polypedilum cf. *tuberculum*	0.8913	0.3582	0.0076*	0.0025*	0.0000*	0.0000*
Psectrocladius cf. *simulans*	0.3720	0.2784	0.2306	0.4532	0.6829	0.3622
Robackia cf. *demeijerei*	0.0008*	0.0006*	0.0026*	0.0250*	0.0000*	0.0000*
Saetheria cf. *tylus*	0.1279	0.0749	0.0010*	0.0526	0.4705	0.1402

with fine sand–very fine sand (Table 5). Occurrence was most clearly related to depressed levels of coarse sand, increased amounts of fine sand, and varying quantities of very fine sand.

Eleven species occurred in strong conjunction with substrates in which very fine sand was >11% and in which amounts of coarse and fine sands were variable (Table 5). Of these 11 species, *Polypedilum* cf. *tuberculum*, *H.* cf. *changi*, *H.* cf. *pilipes*, and *Micropsectra* sp. occurred occasionally in substrates in which coarse sand was >15% concurrently with very fine sand in excess of 11%. The remaining seven species, *Cryptochironomus* sp. 2, *P. camptolabis*-gr., *Cladotanytarsus* sp., *Orthocladius* cf. *obumbratus*, *Paracladopelma* cf. *winnelli*, *P.* cf. *scalaenum*, and *Monodiamesa* cf. *tuberculata* were collected most frequently and numerously in substrates in which very fine sand was >11%, fine sand was variable, and coarse sand was <15%.

Discussion

The distribution and abundance of Chironomidae is controlled by many factors (habitat resource and food availability, predation, reproductive success, competition, and natural mortality). An often neglected factor is morphology, which we postulate is important in controlling the occurrence of the observed species. The size and shape of both the body and head help delimit occurrence. *Cryptochironomus* sp. 1 and *R.* cf. *demeijerei*, which were largely restricted to coarser sediments at 3 and 6 m, have very slender bodies, narrow heads, and tough outer body integuments. In an environment in which the substrate is subject to frequent, violent suspension, a body type enhancing quick substrate penetration is advantageous for reestablishing position in the embenthic habitat. This body morphology also minimizes the erosional effect of sand grains on the body and aids penetration and movement in the shifting, loosely packed sand grains. Sparcity of these two taxa in substrates with very fine sand in excess of 11% may be related to an inability to quickly penetrate and move in the more densely packed, finer sediments.

Chironomid species such as *S.* cf. *tylus*, *P.* cf. *simulans*, *Cryptochironomus* sp. 3, and *C.* cf. *rolli* inhabited sediments with variable concentrations of coarse and fine sands but which were concurrently low in very fine sand. The major portion of their respective populations resided in the coarse substrates but had an expanded habitat range into slightly finer substrates. All of these species except *S.* cf. *tylus* were more robust and larger than were taxa most strongly associated with coarse sand. Increased size may enable these species to burrow efficiently in the more closely packed sands.

Chironomus fluviatilis-gr. was strongly associated with substrates consisting largely of fine sand and was not negatively associated with very fine sand as were the previous six taxa. Occurrence of *C. fluviatilis*-gr. primarily in fine sand, but also in conjunction with very fine sand, indicates that it is transitional between the species closely associated with coarse sand and those closely associated with very fine sand. Being the largest and most robust species, *C. fluviatilis*-gr. is likely able to burrow into any of the substrates available in the survey area. However, because it is tubicolous, establishing a tube in nearshore coarse substrates may limit its occurrence, since these substrates are subject to frequent change due to storm activity. In this case, it is advantageous to inhabit stable sediments to reduce excessive energy expenditure needed to reestablish tubes destroyed by frequently disturbed substrates. Nonetheless, since *Chironomus* develops quickly in the warm water of summer months and storm activity is minimal, sizable densities may occur in the nearshore, coarser substrates during periods of tranquil weather.

The remaining 11 chironomid taxa occurred in strong

TABLE 5. Percent frequency of occurrence (%FO) among samples below and above the median value (<MV and >MV, respectively) for each substrate type. Average densities expressed as No. $\cdot$ m^{-2} and are given in parentheses. N = No. of samples.

		Substrate type						
		$<2\phi$ MV = 15%		$2-3\phi$ MV = 58%		$\geq 3\phi$ MV = 11%		
Taxon	Density	%FO <MV	%FO >MV	%FO <MV	%FO >MV	%FO <MV	%FO >MV	N
Chironomus fluviatilis-gr.	Absent	41	59	58	42	51	49	291
	Present	61(161)	39(126)	41(106)	59(181)	49(141)	51(146)	249
Cladotanytarsus sp.	Absent	44	56	54	46	55	45	436
	Present	74(99)	26(17)	32(26)	68(90)	29(18)	71(98)	104
Cryptochironomus rolli	Absent	48	52	52	48	49	51	447
	Present	57(15)	43(26)	42(25)	58(17)	54(22)	46(20)	93
Cryptochironomus sp. 1	Absent	53	47	49	51	48	52	500
	Present	17(3)	83(25)	60(20)	40(7)	80(25)	20(3)	40
Cryptochironomus sp. 2	Absent	32	68	55	45	65	35	282
	Present	69(123)	31(36)	45(64)	55(95)	34(53)	66(106)	258
Cryptochironomus sp. 3	Absent	49	51	50	50	49	51	495
	Present	58(7)	42(5)	47(6)	53(7)	62(9)	38(4)	45
Heterotrissocladius cf. *changi*	Absent	48	52	46	54	58	42	439
	Present	57(26)	43(23)	65(35)	35(14)	17(12)	83(38)	101
Hydrobaenus cf. *pilipes*	Absent	50	50	47	53	54	46	460
	Present	47(17)	53(43)	65(51)	35(9)	29(22)	71(37)	80
Micropsectra sp.	Absent	50	50	49	51	51	49	494
	Present	52(24)	48(27)	59(39)	41(13)	35(14)	65(38)	46
Monodiamesa cf. *tuberculata*	Absent	48	52	44	56	60	40	401
	Present	55(32)	45(26)	68(43)	32(15)	20(11)	80(47)	139
Orthocladius cf. *obumbratus*	Absent	46	54	52	48	53	47	413
	Present	61(34)	39(26)	42(28)	58(33)	42(32)	58(29)	127
Paracladopelma camptolabis-gr.	Absent	34	66	61	39	59	41	236
	Present	62(356)	38(160)	41(196)	59(320)	43(233)	57(283)	304
Paracladopelma cf. *winnelli*	Absent	48	52	49	51	53	47	461
	Present	63(14)	37(8)	57(13)	43(10)	34(8)	66(15)	79
Polypedilum cf. *scalaenum*	Absent	37	63	52	48	63	37	308
	Present	67(191)	33(75)	48(114)	52(152)	32(54)	68(212)	232
Polypedilum cf. *tuberculum*	Absent	50	50	47	53	55	45	460
	Present	47(12)	53(24)	65(26)	35(10)	19(10)	81(26)	80
Psectrocladius cf. *simulans*	Absent	51	49	50	50	50	50	454
	Present	46(18)	54(273)	51(249)	49(42)	52(264)	48(27)	86
Robacki cf. *demeijerei*	Absent	56	44	47	53	43	57	339
	Present	41(85)	59(280)	56(236)	44(129)	61(304)	39(60)	201
Saetheria cf. *tylus*	Absent	45	55	55	45	47	53	191
	Present	52(211)	48(562)	47(559)	53(214)	52(487)	48(286)	349

association with substrates having very fine sand in excess of 11%. Increased amounts of very fine sand suggest increased stability in the benthic environment. In conjunction with increased environmental stability, a great variety of body shapes and sizes was observed among the chironomids. Some species were large, free-living, embenthic burrowers with tough body integuments and heads well adapted for penetration (*M.* cf. *tuberculata*, *Cryptochironomus* sp. 2, *P.* cf. *winnelli*). Although smaller in size, *P. camptolabis*-gr. was similar in morphology. Other species were variously sized, soft bodied, and tubicolous (*Cladotanytarsus* sp., *Micropsectra* sp., *H.* cf. *changi*). Although these 11 species were strongly associated with very fine sand, there was increased variety in substrate associations not as evident among the previously considered 7 species. Four species (*P.* cf. *tuberculum*, *H.* cf. *changi*, *H.* cf. *pilipes*, and *Micropsectra* sp.) strongly associated with very fine sand also occurred concurrently in sediments with coarse sand in excess of 11%. However, they did not occur frequently in the nearshore coarse substrates, which had low quantities of very fine sand, but rather, they occurred in substrates farther offshore (12 and 15 m) where there was a nearly equal mix of very fine sand and coarse sands. This trend clearly differentiated them from the nearshore species, which were negatively associated with very fine sand.

The richness of body shape, size, and behavior of chironomids at 9–15 m was evidence of an increased degree of stability in the benthic environment not present at 3 and 6 m. Species occurring primarily where substrates are subject to frequent change were morphologically adapted for an ephemeral benthic environment. None of the tubicolous forms occurred in strong conjunction with nearshore, coarse-sand substrates. Rather, these forms, along with other free-living forms, inhabited finer sand substrates or offshore mixtures of very fine- and coarse-sand substrates.

The reasons why tubicolous forms orient toward a stable, more finely sedimented benthic environment seem straightforward. Among tube builders it is easier to build tubes and filter feed or forage in an area where the likelihood of frequent change and destruction of the tube is reduced. However, the reasons why free-living embenthic forms that dominate the nearshore chironomid fauna exhibit specific substrate associations are complex.

Two important factors not related to morphology that may prevent free-living species from successfully establishing populations in different sediment types are food resource and feeding mechanisms. For predacious species, food may be reduced or unavailable in certain substrates. *Cryptochironomus* sp. 2, which is predacious on oligochaetes, would likely establish itself in substrates most hospitable to oligochaetes, that being finer sands as opposed to coarser sands. For species feeding primarily by ingesting sand grains (*S.* cf. *tylus*, *R.* cf. *demeijerei*, *P. camptolabis*-gr., *Cryptochironomus* sp. 1), either the availability of ingestible grain size or the food resources associated with them may be limiting factors. Because sediments in our survey area were a diverse collection of grain sizes, availability of ingestible grain sizes seems limitless. Consequently, the type of food or its availability functions to differentiate the taxa into substrate associations.

However, a factor directly related to morphology is the ability of the chironomid to penetrate a substrate. Among lotic chironomids, as the mean head capsule width-to-grain size ratio approaches unity, the ability to penetrate and burrow decreases (Wiley 1980). It follows, when penetration time increases, that time spent in the epibenthic or pelagic environments increases the probability of predation or being swept into less hospitable locations. In environments frequently disturbed by wave activity, the number of times an individual is dislodged from the sediment is also increased. Increased time in the water column increases the chances of predation and contact with inhospitable locations. Assuming the availability of both large and small species and that larger species are more susceptible to predation than are smaller species, it is particularly advantageous for larger species to occur in a stable environment where the above factors are not as operative, thereby reducing their chances of exposure to inhospitable habitats and fish predation. We postulate that the morphology (small, slender, fast, tough outer body integuments) of the species most strongly associated with coarse sands is a significant factor affecting why remaining species do not have significant occurrences in these sediments. On the other hand, morphological characteristics (generally larger, thicker, slower, more robust, some soft bodied, and tubicolous) of remaining species make them more successful where lake processes are less intense and penetration is less exacting and frequent.

Food availability, penetration of substrates, exposure to predation, and stability of habitat differentiate the free-living, embenthic species into the substrate associations observed. Clearly, other factors may be operative, e.g. competition. Factors considered in this paper provide hypotheses that in part explain some of the differences. Hopefully, these hypotheses will encourage research focusing on the extent to which morphology and physical capabilities affect the ability of chironomids to use different substrates. Increased knowledge of fish predation, competition, and food preferences will greatly enhance interpretation of substrate preference, but morphological characteristics are important because they establish the physical limitations of the species.

Acknowledgments

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Transport of Dissolved Organic Carbon, Nutrients, and Trace Metals from the Wilson and Blossom Rivers to Smeaton Bay, Southeast Alaska[1]

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Sugai, S. F., and D. C. Burrell. 1984. Transport of dissolved organic carbon, nutrients, and trace metals from the Wilson and Blossom rivers to Smeaton Bay, southeast Alaska. Can. J. Fish. Aquat. Sci. 41: 180–190.

Regional and seasonal differences in chemical input from the Wilson and Blossom rivers, two pristine, major salmon-producing rivers in southeast Alaska, were examined. For a period of 2 yr, concentrations of dissolved organic carbon, nutrients, Cu, Fe, and Mn in the rivers were determined at approximately monthly intervals and used to calculate export rates. Because of extremely high annual precipitation (400–450 cm) and drainage basins restricted by high topographical relief, the concentrations and export rates of nutrients and Cu are low in the rivers for most of the year. The maximum nutrient export from the Wilson–Blossom system appears to be closely tied to the annual salmon cycle. Iron and Mn export rates from the watersheds are much higher than those for Cu, reflecting solubilization of Fe and Mn under reducing conditions that develop in muskeg ponds during drought periods. The association of metals with organics allows transport of Fe and possibly other metals throughout the fjord system, in contrast with the large-scale removal of metals in or near the river's mouth, as has been observed elsewhere.

Les auteurs ont étudié les différences régionales et saisonnières entre les apports chimiques des rivières Wilson et Blossom, deux importantes rivières sauvages productrices de saumons, situées au sud-est de l'Alaska. Pendant 2 ans, ils ont déterminé les concentrations de carbone organique, de bioéléments, de Cu, de Fe et de Mn dissous dans ces eaux, à des intervalles d'environ un mois. Ces résultats ont servi au calcul des taux d'exportation. À cause des très fortes précipitations annuelles (de 400 à 450 cm) et du relief topographique élevé des bassins de drainage, les rivières connaissent de faibles concentrations et taux d'exportation de bioéléments pendant la plus grande partie de l'année. Il semble que l'exportation maximum d'éléments nutritifs du système Wilson–Blossom soit reliée de près au cycle annuel du saumon. Les taux d'exportation du Mn et du Fe des bassins versants sont beaucoup plus élevés que ceux de cuivre, ce qui traduit la solubilisation du Fe et du Mn en présence du potentiel réducteur qui se développe dans les fondrières pendant les périodes de sécheresse. L'association de métaux avec des matières organiques permet le transport du Fe et peut-être d'autres métaux dans tout le système de fjords, contrairement à ce qui a été observé ailleurs, c'est-à-dire l'enlèvement à grande échelle des métaux à l'embouchure ou près de l'embouchure fluviale.

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The salmon fisheries of southeast Alaska are a resource of enormous commercial, subsistence, and recreational value. However, in the decade ahead, mining and logging developments within the watersheds of natural salmon rivers will present inevitable management conflicts for fisheries officials. Because the structure of a stream ecosystem is determined by characteristics of its drainage network (Hynes 1975; Vannote et al. 1980), altered land usage can upset the existing biotic regulation of hydrological and biogeochemical characteristics (Bormann and Likens 1979). A fluctuating water regime can destabilize streambed composition and geomorphology causing increased erosion and siltation. This reduces the quality of food (Sloane-Richey et al. 1981) and habitat (Naiman and Sedell 1981) for salmonid fishes. In addition, significant changes in the availability of carbon, nutrients, and trace metals to the stream system could alter the number of salmon migrating to the estuary and beyond.

In 1980 when we began this study we found no literature on the chemistry of any of the over 2000 salmon-producing streams in southeast Alaska. Because increasing development poses an immediate threat to an enormously important fisheries resource, there was a pressing need to determine the biological and chemical cycles present in this environment. A thorough study of a pristine salmon river from a watershed perspective would be valuable to fisheries managers responsible for reestablishing historical salmon runs, enhancing depleted stocks by artificial propagation, and managing natural streams. This study represents a first attempt at quantifying some of the chemical exports occurring in a natural salmon stream. To do this, we examined the annual transport of dissolved organic carbon, nutrients, and trace metals from the Wilson and Blossom rivers.

Because our objective was to examine the transport of dissolved substances from the Wilson–Blossom river system that were relevant to salmonid habitat, we limited our scope to chemical variables that would yield the most information and serve as models for unmeasured chemical species. Hence, we studied the carbon and nutrient exports to determine possible

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[1] Contribution No. 533, Institute of Marine Science, University of Alaska, Fairbanks, AK.

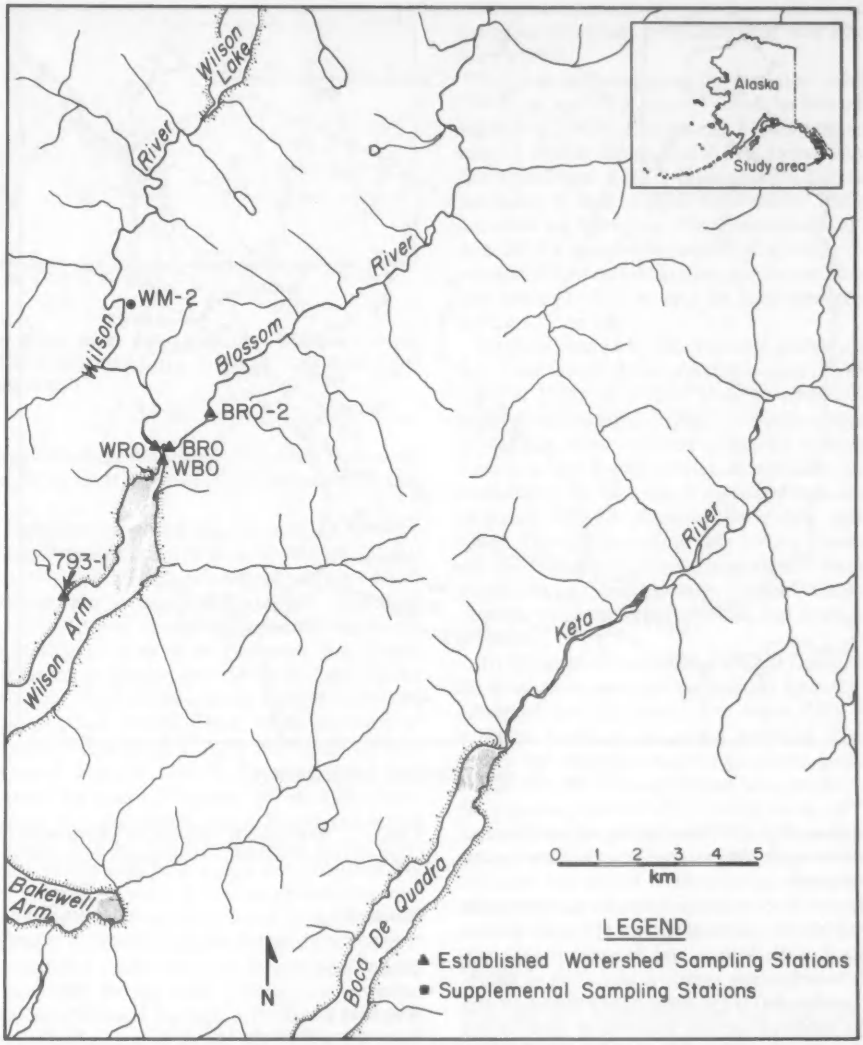
Wilson Lake
Wilson River
Blossom River
WM-2
BRO-2
WRO
BRO
WBO
793-1
Wilson Arm
Keta River
Bakewell Arm
Boca De Quadra
Alaska
Study area
N
0 1 2 3 4 5
km
LEGEND
▲ Established Watershed Sampling Stations
■ Supplemental Sampling Stations

FIG. 1. Location of study sites on the Wilson–Blossom river system and in the watershed of Smeaton Bay.

restraints on productivity, and the trace metals to examine transport mechanisms of potential toxicants. Copper was selected for detailed examination because although it is utilized by phytoplankton as a micronutrient, at elevated concentrations several soluble Cu species are toxic to microfauna and higher organisms including fish (e.g. Whitfield and Lewis 1976; Lorz and McPherson 1976; Chakoumakos et al. 1979). Iron and Mn were also chosen for study because of their involvement in redox-coupled reactions and because hydrated ferric oxides and manganese dioxides can be important scavenging agents for heavy metals (Lion et al. 1982; Olsen et al. 1982).

Study Area

The Wilson–Blossom river system (55°24.8′N, 130°36.4′W) is located in a rugged mountainous region approximately 28 km northeast of Ketchikan, Alaska (Fig. 1). The high relief limits the river drainage area and minimizes the response time of the river to events occurring in the watershed. The natural vegetation is dominated by a dense forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with extensive regions of poorly drained muskeg. The region is characterized by cool summers, mild winters, and heavy precipitation. Normal annual precipitation is 400–450 cm (USDA Forest Service 1979), with October and November usually the wettest months. At sea level most precipitation is in the form of rain although at higher elevations snow accumulates between December and April. The Wilson and Blossom rivers meet about 0.8 km from Wilson Arm at the head of Smeaton Bay (Fig. 2), a steep-walled, glacially formed fjord. Physical and chemical characteristics of the rivers are given in Table 1. Both the Wilson and Blossom rivers experience spring freshets in May–June when accumulated snow begins melting at higher elevations and strong autumn freshets (September–November)

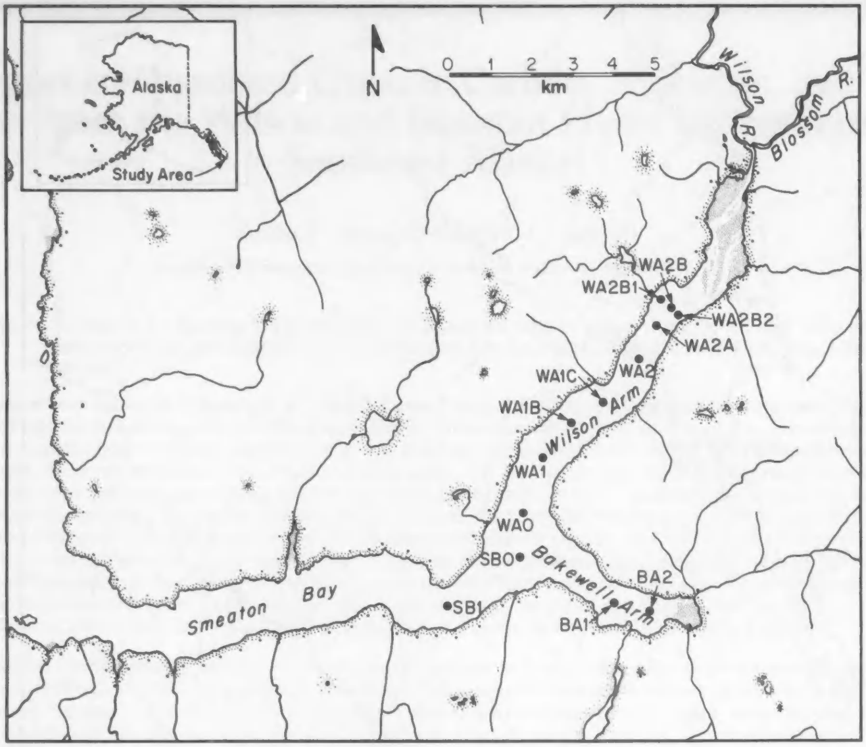

FIG. 2. Location of stations in Smeaton Bay.

during the rainy season (Fig. 3). Flows during winter (December–April) and late summer (August) are generally low except during occasional storms.

The Wilson-Blossom river system is a natural salmon stream system. Four of five North American species of Pacific salmon are commonly found in the Wilson and Blossom rivers; only sockeye salmon (*Oncorhynchus nerka*) is rare. Pink or humpback salmon (*O. gorbuscha*) is the numerically dominant and commercially most important species, followed by chum or dog salmon (*O. keta*), coho or silver salmon (*O. kisutch*), and chinook or king salmon (*O. tshawytscha*).

Materials and Methods

Sampling Methods

From June 1980 to August 1982, stations on the Wilson Blossom rivers and at selected sites in the watershed of Smeaton Bay (Fig. 1) were sampled at approximately monthly intervals for dissolved organic carbon (DOC) and dissolved nutrients; samples for Cu, Fe, and Mn were routinely collected beginning March 1981.

To minimize the effects of tidal variations in trace elements (Boyden et al. 1979), we sampled the rivers within 2 h of high tide. Unfiltered samples were collected approximately 0.5 m below the surface in an upstream direction as far as possible away from the shore and skiff.

Early results demonstrated the need for extreme caution against contamination in DOC and trace metal samples. Because of the potential for contamination, most of the trace metal samples were collected unfiltered. We adopt the convention of Boyle et al. (1977b) and report metal concentrations as "acid soluble," or those metals in the sample that are converted to a labile form by acidification to less than pH 2. River trace metal samples were collected directly into linear polyethylene (LPE) sample bottles that had been acid cleaned for 1 wk with 6 mol HCl·L^{-1}, soaked with quartz double-distilled water (Q water) for several weeks during which the rinse water was changed at least four times, and dried at room temperature in a laminar flow hood (Environmental Air Control, Inc.) in a clean room. Acid-washed LPE sample bottles were opened below the water surface (to avoid contamination from the surface film),

TABLE 1. Physical and chemical characterization of rivers.

Parameter	WRO Wilson River	BRO Blossom River
Stream order[a]	3	3
Links[b]	26	20
Watershed area (km^2)	294	181
Mean annual discharge (m^3·s^{-1})	33.0[c]	20.2[c]
Gradient (%)	1.45	2.52
Proportion of basin above tree line (%)	42	51
pH (June 3, 1982)	5.8	6.9

[a] Strahler (1957).
[b] Shreve (1966).
[c] USDA Forest Service (1982).

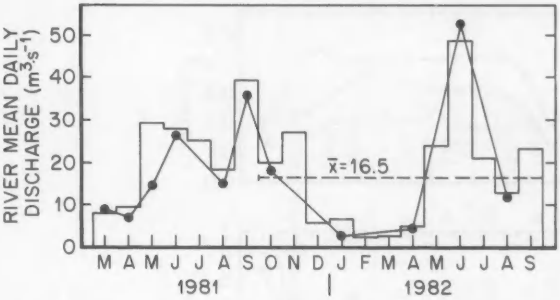

FIG. 3. Blossom River mean daily discharge. Histogram shows monthly mean value for daily discharge. Points show mean daily discharge on sampling dates.

rinsed three times, filled approximately two-thirds full, acidified with Ultrex HCl (Baker Chemical Co.), and stored frozen until analysis.

River water samples for dissolved Cu and DOC were collected from below the surface with an acid-cleaned, 20-mL all-glass syringe. Two syringe volumes (40 mL) of river water were forced through the syringe and discarded. The third syringe volume (20 mL) was forced through two combusted Whatman EPM 1000 glass fiber filters preloaded in a 25-mm diameter, acid-cleaned polypropylene Swinnex filter holder (Millipore Corp.). Use of two filters allowed using the Swinnex holder without the supplied silicone gasket, which was found to be a source of metal contamination. After discarding the first 20 mL of river water that was filtered, the next 40 mL was collected for Cu analyses in an acid-cleaned, 60-mL LPE bottle, acidified with Ultrex HCl, and stored frozen. Samples collected for DOC were filtered directly into precombusted 20-mL glass ampules that were immediately heat sealed and refrigerated in darkness prior to processing. As a precaution against overloading the filters, no more than 60 mL was filtered through a given filter set, and if visual inspection indicated substantial particulate material accumulating on the filter (the Swinnex holders are transparent), a new filter set was used. Samples for inorganic nutrient analyses were filtered through a 0.45-μm Millipore filter and frozen for subsequent analysis.

Analytical Methods

DOC and POC samples were sealed into 10-mL precombusted ampules on board ship along with 0.2 g of $K_2S_2O_8$ and 0.25 mL of 6% H_3PO_4 using a modification of the persulfate oxidation method of Strickland and Parsons (1972). To minimize procedural blanks of 0.2–0.5 mg $C \cdot L^{-1}$, we made a series of three standard additions of dextrose in duplicate or triplicate to each DOC sample and a linear regression made for the 10 points obtained. For POC samples, at each station four replicates were filtered through preashed Gelman glass fiber filters and sealed with $K_2S_2O_8$, H_3PO_4, and 5 mL of Q water added with a glass repipette. Samples were compared with dextrose standards added to ampules containing a preashed filter and the other reagents.

Dissolved inorganic and total nutrients were determined by autoanalyzer. For ammonia, the method used was that of Koroleff (1970). Nitrite was determined by the Greiss reaction, as described by Armstrong et al. (1967). Nitrate is quantitatively reduced to nitrite using copperized Cd filings. The inorganic phosphate procedure used was that of Murphy and Riley (1962).

Iron was analyzed using the ferrozine technique of Stookey (1970), as applied to natural waters by Murray and Gill (1978) and Gibbs (1979). Copper and Mn determinations were made using a Perkin-Elmer model 360 atomic absorption spectrophotometer and a HGA 2100 graphite furnace. At least three injections of each sample were made. The relative standard deviation for Mn using 25-μL injections was consistently less than 5% for samples between 0.8 and 8 $\mu g \cdot L^{-1}$. The relative standard deviation for Cu using one or two 50-μL injections was approximately 15% or less for concentrations in the range of 0.5 $\mu g \cdot L^{-1}$ or less.

Daily discharge by the Blossom River was gauged by the U.S. Geological Survey at a station established on February 11, 1981, at 55°25.34′N, 130°33.40′E, roughly 1.5 km upstream from our station BRO-2 (Fig. 1). To obtain discharge values for the Wilson River we used computed synthetic-flow data (L. Bartos, USDA Forest Service, Ketchikan, AK, personal communication) for both the Wilson and Blossom rivers to adjust measured 1981–82 Blossom River flow data for the Wilson River. The synthetic flow data were generated from input of precipitation, drainage area, proportion of basin above tree line, proportion of basin in main channel lakes, slope of main channel, mean elevation of basin, and south distance to Dixon entrance.

To calculate the monthly chemical inputs of the Wilson and Blossom rivers we used the monthly mean daily discharge and measured concentrations. The mean daily discharge of the Blossom River on the actual sampling dates (solid circles) versus the monthly mean (histogram) is shown in Fig. 3. Because of the close agreement between the flow measured on the sampling date and the monthly mean ($R^2 = 0.91$) we feel that our sampling does not reflect anomalous dates within a given month. For months in which no actual samples were collected, we used a mean between the month preceding and following.

Results

DOC and POC Concentrations and Total DOC Export

The DOC concentrations of the Wilson and Blossom rivers exhibit seasonal variations but the annual range is ≤3 mg $C \cdot L^{-1}$ (Fig. 4a). The Wilson River generally has higher DOC concentrations (mean 4.0 ± 1.1 mg $C \cdot L^{-1}$) than the Blossom River (mean 2.5 ± 0.7 mg $C \cdot L^{-1}$).

The POC concentrations in these rivers account for less than 10% of the total carbon. POC values and the DOC:POC ratios for the rivers are shown in Table 2. POC measurements were made in the 1982 field season only and may not represent generalized conditions. The DOC:POC ratios in the Wilson and Blossom rivers were almost identical in April 1982, a low-flow period prior to snowmelt at higher elevations of the watershed. During the high flow period in June, the DOC:POC ratios of the Blossom River (BRO) and the Wilson–Blossom confluence (WBO) decrease, while the ratio for the Wilson River (WRO) increases. In August, another low-flow month, the river DOC:POC ratios are either lower than June (for station WRO) or nearly the same (BRO and WBO).

The transport of DOC from the rivers to the fjord is bimodal, with 30% of the annual Blossom River DOC export (Table 3) occurring in May and June and 37% in September–November.

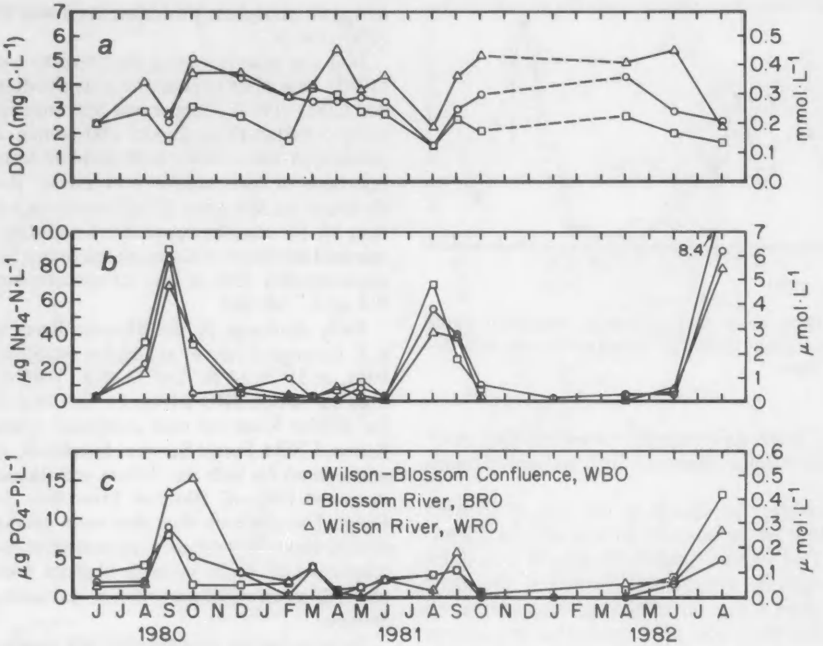

FIG. 4. (a) Dissolved organic carbon versus time for the Wilson–Blossom confluence, Blossom River, and Wilson River; (b) dissolved ammonia versus time; (c) dissolved inorganic phosphate versus time.

TABLE 2. POC values and DOC:POC ratios for river stations, 1982. Data are means of four determinations ±1 SD.

		April		June		August	
Station	Location	POC (mg C·L⁻¹)	DOC:POC	POC (mg C·L⁻¹)	DOC:POC	POC (mg C·L⁻¹)	DOC:POC
WBO	Wilson–Blossom confluence	0.14±0.01	30.7	0.18±0.03	15.9	0.16±0.01	15.6
WRO	Wilson River	0.22±0.02	22.6	0.15±0.02	36.3	0.19±0.01	12.1
BRO	Blossom River	0.12±0.01	21.4	0.21±0.02	9.8	0.15±0.01	10.4
BRO-2	Blossom River, upstream			0.16±0.01	16.7	0.15±0.02	10.9

For the Wilson River (Table 4) 22% of the annual export occurs in May and June and 44% in the three autumn months. Thus, for the year between March 1981 and February 1982, the Wilson River contributed 3.25×10^8 mol of DOC, while the Blossom River exported 1.19×10^8 mol. As shown in Table 5 the annual DOC export per unit area of watershed for the Wilson River ($13.3\,g\,C \cdot m^{-2} \cdot yr^{-1}$) is greater than for the Blossom River ($7.9\,g\,C \cdot m^{-2} \cdot yr^{-1}$).

Nitrogen and Phosphorus Concentrations and Annual Exports

There are distinct seasonal variations in dissolved inorganic nitrogen and phosphorus concentrations in the Blossom and Wilson rivers. Ammonia is extremely low ($<1\,\mu mol \cdot L^{-1}$) at the three main river stations (Fig. 4b), with peak concentrations of $4\text{–}6\,\mu mol \cdot L^{-1}$ occurring in late summer–early fall. Phosphate concentrations (Fig. 4c) are near analytical detection limits during most of the year except in late summer–autumn. Nitrate + nitrite has a less noticeable seasonal cycle, with concentrations generally rising through the fall–winter season.

The monthly river export rates for nitrate + nitrite (Table 3) are highest for the Blossom River in September 1981, a period of high mean daily discharge. Likewise, for the Wilson River (Table 4) the highest nitrate + nitrite export rates (September and November 1981) correspond with peak discharge rates. However, for ammonia the export increases in both rivers prior to the high-flow times. The maximum phosphate export from the Wilson and Blossom rivers occurs in September. The annual nutrient exports per unit watershed area are tabulated for the Wilson and Blossom rivers in Table 5.

Annual Concentrations and Exports of Cu, Fe, and Mn

Because of highly leached soils and high discharge rates, the concentrations of acid-soluble Cu are extremely low (less than $0.7\,\mu g \cdot L^{-1}$ or $11\,nmol \cdot L^{-1}$) (Fig. 5). Based on a limited number of samples (Fig. 5b) the particulate Cu phase appears to be more important for Blossom River than for the Wilson River. However, because of the extremely low levels of acid-soluble Cu, it is difficult to discern spatial differences.

TABLE 3. Monthly chemical input from the Blossom River into Wilson Ar

	Mar.	Apr.	May	June	July
DOC (10^6 mol)	6.7	7.5	18.8	16.6	12.1
$NO_3 + NO_2$ (10^3 mol)	152	199	488	252	232
NH_4 (10^3 mol)	5.3	11.4	59.5	10.8	167
PO_4 (10^3 mol)	2.8	0.75	3.1	5.7	5.3
Cu (10^3 mol)	0.07	0.06	0.43	0.46	0.37
Fe (10^3 mol)	34	54	213	117	131
Mn (10^3 mol)	1.8	2.6	7.3	4.7	6.1

TABLE 4. Monthly chemical input from the Wilson River into Wilson Arm

	Mar.	Apr.	May	June	July
DOC (10^6 mol)	12.3	19.7	36.7	39.6	26.8
$NO_3 + NO_2$ (10^3 mol)	130	169	464	31	88
NH_4 (10^3 mol)	7.5	24.9	28.7	12.8	276
PO_4 (10^3 mol)	4.5	0.86	0.0	7.5	4.8
Cu (10^3 mol)	0.18	0.09	0.60	0.33	0.36
Fe (10^3 mol)	74	117	330	121	110
Mn (10^3 mol)	2.9	3.8	10.2	5.5	5.1

ilson Arm, March 1981–February 1982.

July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Annual export
12.1	5.9	22.3	9.6	12.4	2.7	3.0	1.0	119
32	171	1520	250	476	103	118	38	4000
67	239	178	24.4	23.6	5.1	5.9	1.9	732
5.3	4.4	11.2	1.1	1.4	0.29	0.35	0.12	36.5
0.37	0.22	0.69	0.26	0.36	0.08	0.09	0.03	3.12
31	113	394	89	142	31	35	11	1360
6.1	5.7	18.1	5.2	7.4	1.6	1.8	0.6	62.9

son Arm, March 1981–February 1982.

July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Annual export
26.8	14.7	60.6	37.8	47.1	11.5	13.9	4.0	325
88	120	505	191	505	123	148	43	2520
276	212	239	17.6	18.4	4.4	5.4	1.6	848
4.8	2.3	29.5	0.0	2.4	0.56	0.67	0.19	53.3
0.36	0.34	0.85	0.62	0.67	0.16	0.20	0.06	4.46
110	89	370	183	247	60	73	21	1800
5.1	4.3	8.6	6.9	8.6	2.1	2.5	0.7	61.2

TABLE 5. Annual chemical export per unit area for watersheds, March 1981–February 1982.

		Blossom River (this study)	Wilson River (this study)	Nanaimo River (Naiman and Sibert 1978)
DOC	$mol \cdot m^{-2} \cdot yr^{-1}$	0.66	1.1	
	$g\,C \cdot m^{-2} \cdot yr^{-1}$	7.9	13.3	14.5
$NO_3 + NO_2$	$mmol \cdot m^{-2} \cdot yr^{-1}$	22	8.6	
	$mg\,NO_3\text{–}N \cdot m^{-2} \cdot yr^{-1}$	310	120	73
NH_4	$mmol \cdot m^{-2} \cdot yr^{-1}$	4.0	2.9	
	$mg\,NH_4\text{–}N \cdot m^{-2} \cdot yr^{-1}$	57	40	190
PO_4	$mmol \cdot m^{-2} \cdot yr^{-1}$	0.20	0.18	
	$mg\,PO_4\text{–}P \cdot m^{-2} \cdot yr^{-1}$	6.2	5.6	
Cu	$mmol \cdot m^{-2} \cdot yr^{-1}$	0.017	0.015	
	$mg\,Cu \cdot m^{-2} \cdot yr^{-1}$	1.1	0.96	
Fe	$mmol \cdot m^{-2} \cdot yr^{-1}$	7.5	6.1	
	$g\,Fe \cdot m^{-2} \cdot yr^{-1}$	0.42	0.34	
Mn	$mmol \cdot m^{-2} \cdot yr^{-1}$	0.35	0.21	
	$mg\,Mn \cdot m^{-2} \cdot yr^{-1}$	19	11	

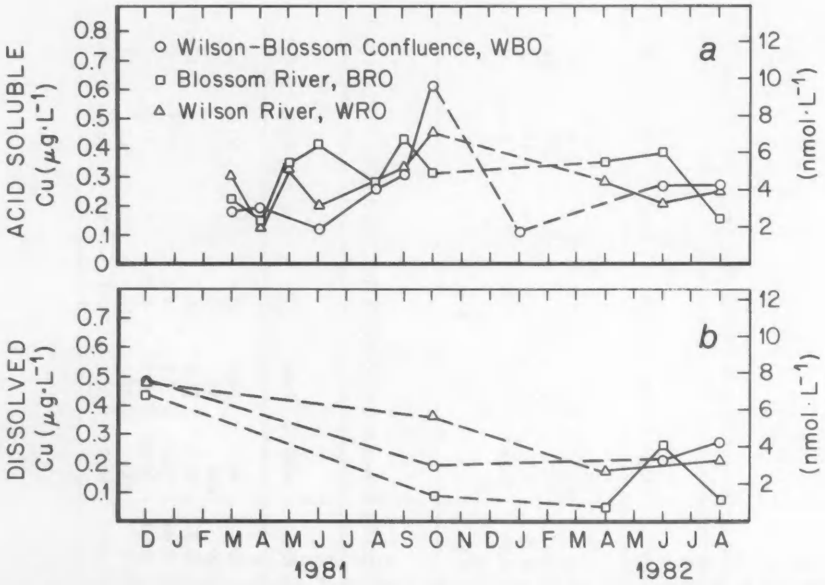

FIG. 5. (a) Acid-soluble Cu versus time for the Wilson–Blossom confluence, Blossom River, and Wilson River; (b) dissolved Cu versus time.

The seasonal export of Cu reflects the small concentration range for the metal and its apparent dependence on flow. For the Blossom River, 40% of the annual transport occurs during May–July and an additional 22% is removed in September (Table 3). In the Wilson River, the export of Cu initially peaks in May, decreases somewhat during June–August, then increases dramatically in September and remains high through November. During the autumn period 48% of the annual Cu load of the Wilson River is carried to Smeaton Bay (Table 4). As shown in Table 5, the annual acid-soluble Cu exports per unit area for the Blossom and Wilson watersheds for the year March 1981–February 1982 are virtually identical ($1.1\ mg\,Cu \cdot m^{-2} \cdot yr^{-1}$ for the Blossom River and $0.96\ mg\,Cu \cdot m^{-2} \cdot yr^{-1}$ for the Wilson River). In addition, if data primarily from the 1982 field season are used to calculate annual export rates (September 1981–August 1982), the results are unchanged. For the latter period, the Cu export rate for the Blossom River is $1.1\ mg\,Cu \cdot m^{-2} \cdot yr^{-1}$ and for the Wilson River is $0.91\ mg\,Cu \cdot m^{-2} \cdot yr^{-1}$.

The curves of acid-soluble Fe (Fig. 6a) and acid-soluble Mn (Fig. 6b) versus time are very similar. The dominant peak in concentration for both Fe and Mn occurs in September–October when the autumn rains flush the watershed.

The export rates of acid-soluble Fe from the Blossom and Wilson rivers have sharp peaks in May and September, reflecting the seasonal peaks in concentration as well as flow. Sixteen percent of the Blossom River export of Fe occurs in May and 29% in September. In the Wilson River, the Fe transport rate can be grouped as follows: 18% in May and 44% between

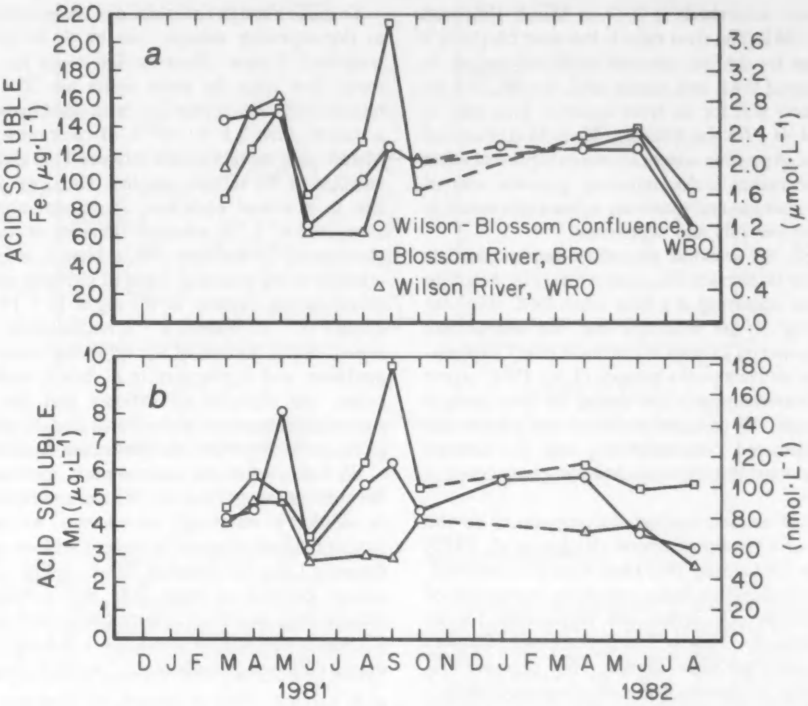

FIG. 6. (a) Acid-soluble Fe versus time for the Wilson–Blossom confluence, Blossom River, and Wilson River; (b) acid-soluble Mn versus time for the Wilson–Blossom confluence, Blossom River, and Wilson River.

September and November. The annual Fe export for the Blossom River is 0.42 $g\,Fe \cdot m^{-2} \cdot yr^{-1}$ and for the Wilson River is 0.34 $g\,Fe \cdot m^{-2} \cdot yr^{-1}$.

The Mn export from the Blossom River is greatest in September (29%). For the Wilson River 17% of the Mn export occurs in May, 14% in September, and 14% in November. However, the export rates remain relatively high throughout the summer and fall for both rivers. The annual Mn export rate for March 1981–February 1982 is 19 $mg \cdot m^{-2} \cdot yr^{-1}$ for the Blossom River and 11 $mg\,Mn \cdot m^{-2} \cdot yr^{-1}$ for the Wilson River.

Discussion

Dissolved and Particulate Carbon

Although mean DOC concentrations for the Wilson and Blossom rivers are less than the world average of 5.75 $mg\,C \cdot L^{-1}$ (Meybeck 1982), high discharge rates from relatively small basins result in a high DOC export to Wilson Arm and Smeaton Bay. The DOC exports of the Wilson and Blossom rivers are exceptionally high compared with other North American rivers (Moeller et al. 1979; Schlesinger and Melack 1981). Of systems with comparable watershed areas, only the Nanaimo River, a sixth-order stream on the east coast of Vancouver Island, British Columbia, has transport rates for DOC that are comparable with the rivers we studied. The Nanaimo River, which drains 894 km^2 of mountainous terrain, transports 14.5 $g\,C \cdot m^{-2} \cdot yr^{-1}$ as DOC (Naiman and Sibert 1978), which is roughly equivalent to the export we obtained for the Wilson River. Because the Nanaimo River has some hydrologic characteristics similar to our study area, we have presented chemical exports from this river with those we obtained for the Wilson and Blossom rivers (Table 5).

Of the two rivers we studied, the Wilson River has a lower gradient basin and more watershed area below the tree line (Table 1); this results in the higher DOC concentrations and lower pH values found in the Wilson River. In addition, the DOC:POC ratio for the Wilson River is generally greater than for the Blossom River, suggesting that biological processing of particulate organic material within Wilson Lake may be occurring. The DOC:POC ratios observed in this study are similar to those reported for tundra and wetlands (Schlesinger and Melack 1981).

Nutrients

The seasonal pattern for transport of ammonia, phosphate, and nitrate + nitrite reflects not only the bimodal discharge pattern but also the significant nonweathering source of ammonia and phosphate. The ammonia concentration pattern we observed in the Wilson and Blossom rivers (Fig. 4b) is unlike that in the Nanaimo River (Naiman and Sibert 1978), where maximum ammonia concentrations occur in January and April. The late summer ammonia peaks in the Wilson and Blossom rivers are also seasonally anomalous when one considers the ratio NH_4-N/DIN (where DIN is the total dissolved inorganic nitrogen, NH_4-N + NO_2-N + NO_3-N). Meybeck (1982) determined that a median value of NH_4-N/DIN for unpolluted rivers is likely to be approximately 0.15 and for unpolluted precipitation 0.55. The measured rainfall NH_4-N/DIN ratio for the Wilson–Blossom watersheds is 0.44 in March 1981 and 0.30 in September 1981. The river ratio is less than Meybeck's median value except for the late summer–early fall period. In September 1980, August 1981, and August 1982, the NH_4-N/DIN ratio is approximately 0.6 for all river stations. This ratio is approximately 0.04–0.1 for the Nanaimo River in August and September. Because in pristine waters ammonia is present when nitrogenous organic matter is decomposing, possible sources are terrestrial plant material and spawning salmon that return to these rivers between late July and September.

In 1980 and 1982, the seasonal phosphate pattern parallels ammonia for both the Wilson and Blossom rivers (Fig. 4c), with maximum phosphate occurring at a time when DOC (Fig. 4a) and stream flow (Fig. 3) are relatively low. We believe that decomposition of spawned salmon is the most likely explanation for the observed nutrient peaks because (1) the DOC export from the terrestrial environment is low during the brief drought period in late summer, (2) calculations show that salmon can account for the observed concentrations, and (3) streams without salmon do not exhibit ammonia and phosphate peaks in late summer.

The importance of salmon carcass decomposition on the phosphorus cycles of a subalpine stream (Richey et al. 1975) and an Alaskan lake (Donaldson 1967) has been demonstrated. Richey et al. (1975) calculated that a spawning population of 14 000 sockeye salmon (*O. nerka*) are responsible for an increase of phosphorus of $4.3\ \mu g \cdot L^{-1}$ in Taylor Creek, California, during the period December–March. They reported that this calculated increase compares well with a measured difference of $6\ \mu g \cdot L^{-1}$ between upstream (no salmon) and downstream phosphate. We suggest that the much larger numbers of predominantly pink salmon in the Wilson and Blossom rivers are largely responsible for the August–September increases in nutrient concentrations.

The Alaska Department of Fish and Game conducts aerial surveys of major salmon streams on a weekly or biweekly basis throughout the major spawning period. Their peak escapement numbers represent the highest 1-d count of salmon based on these surveys. The peak escapement values for the 1980 season were 192 000 mixed pink and chum salmon for the Wilson River on August 3(4 d before our August river sampling) and 65 800 for the Blossom River on August 12 (5 d after our sampling). These numbers are somewhat misleading because fish observed in the area seaward of the confluence of the Wilson and Blossom rivers are counted as Wilson River spawners when in fact a significant portion of the fish will spawn in the Blossom River. Thus, the peak escapement numbers may underestimate fish returning to the Blossom River. In the 1981 season, the peak escapement to the Wilson River was 135 000 on August 18 (6 d after our sampling) whereas the Blossom River peak was 51 400 occurring on August 8 (3 d before our sampling). In the 1982 season, the peak escapement for both rivers occurred on August 16 (9 d before our river sampling) and was 188 000 for the Wilson and 116 000 for the Blossom (P. Doherty, Alaska Department of Fish and Game, Ketchikan, AK, personal communication). Because of the large number of fish in the river at one time and because pinks die within a few days after spawning, it is often difficult to discern live from dead fish in aerial surveys. However, to illustrate the rapid demise of the spawning salmon, a foot survey of the Blossom River on August 31, 1981 (23 d after the peak escapement of 51 400), reported 2867 dead salmon out of 6434 total fish (Jones and Dangel 1982).

To make a rough calculation of the potential nutrient flux due to decomposing salmon, we let 3×10^5 fish represent a combined Wilson–Blossom fish count for August 1982. The mean flow rates for these rivers are 20.4 and $12.9\ m^3 \cdot s^{-1}$, respectively. Assuming that most decomposition occurs within a month, then 8.9×10^{10} L of river water will be affected. Mature pink salmon weigh between 1.36 and 3.18 kg and are the smallest of the salmon species. Thus, we assume the average fish in a mixed pink and chum assemblage is 2.3 kg and composed of 1.3% nitrogen (Parsons et al. 1977) and 0.38% phosphorus (Donaldson 1967). Hence, an order of magnitude measure of the potential input of nitrogen and phosphorus from decomposing salmon is $0.1\ mg\,N \cdot L^{-1}$ ($7.2\ \mu mol \cdot L^{-1}$) and $29\ \mu g\,P \cdot L^{-1}$ ($0.9\ \mu mol \cdot L^{-1}$), respectively. Although it can be argued that a portion of the returning salmon is consumed by predators and scavengers (e.g. bears, eagles, ravens, gulls, seals), our calculations indicate that the potential salmon-supplied nitrogen and phosphorus can account for the observed increases in ammonia and phosphate concentrations.

We believe that the salmon must contribute significantly to the nutrient export from the Wilson and Blossom rivers because in addition to our rough calculations, we have not observed a similar nutrient increase in streams without salmon. The stream draining Lake 793 (station 793-1 on Fig. 1) does not support salmon because of steep falls above Wilson Arm but does receive large quantities of terrestrially derived DOC. On August 27, 1982, this station contained a $6.8\ mg\,C \cdot L^{-1}$ as DOC but only $0.05\ \mu mol$ phosphate$\cdot L^{-1}$ and $0.25\ \mu mol$ ammonia$\cdot L^{-1}$.

Trace Metals

Of the three trace metals examined, the river concentrations of acid-soluble Cu were low and flow dependent; the concentrations of acid-soluble Fe and Mn were higher and more seasonally variable than Cu. More of the acid-soluble Cu was in the dissolved form for the Wilson River than for the Blossom River, suggesting that Wilson Lake may retain or solubilize particulate Cu as well as POC. Biological reduction of Mn oxides and Fe oxides during decomposition of organic matter in muskeg ponds is probably responsible for seasonally high river concentrations of Mn and Fe. The highest concentrations of acid-soluble Fe and Mn were obtained from a sample collected at WM-2, a muskeg pond in the Wilson River watershed on October 16, 1981. Conditions in the pond were highly reducing (hydrogen sulfide was present) with much suspended material in the water. On that day, the acid-soluble Fe concentration was $10\,560\ \mu g \cdot L^{-1}$ ($189\ \mu mol \cdot L^{-1}$) and the acid-soluble Mn concentration was $71.5\ \mu g \cdot L^{-1}$ ($1.3\ \mu mol \cdot L^{-1}$).

Effects of River-Derived Organic Matter on Transport of Trace Metals to Smeaton Bay

Evidence to date suggests that the amount and lability of organic material available to rivers and streams draining into Wilson Arm and Smeaton Bay influence the extent of metal transport to, and reactions within, the freshwater–estuarine mixing zone. As shown in Fig. 7, in the absence of primary productivity, dissolved phosphate in the freshwater–estuarine mixing zone can be described by conservative, two end-member dilution processes (Boyle et al. 1974). In samples collected on October 16, 1981, a linear increase in phosphate ($R^2 = 0.90$) is observed with increasing salinity. The behavior of Fe is less clear. Acid-soluble Fe decreases only slightly with increasing salinity (Fig. 7b), in contrast with the large-scale removal of

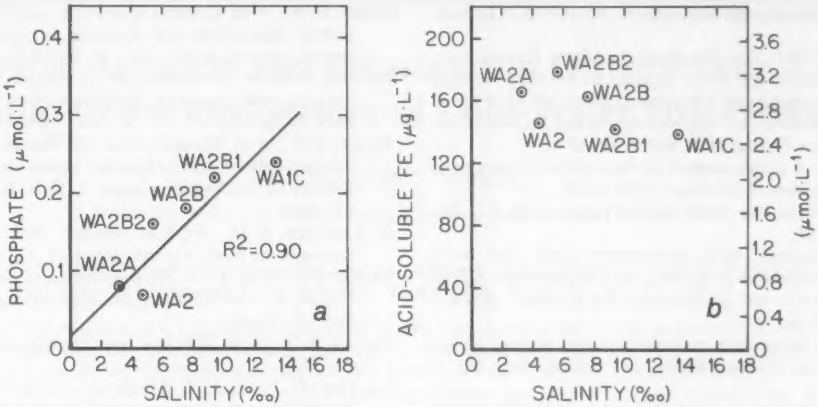

FIG. 7. (a) Dissolved inorganic phosphate versus salinity for stations in Wilson Arm, October 16, 1981; (b) acid-soluble Fe versus salinity.

metals in (Eaton 1979) or near the river's mouth that has been observed elsewhere (e.g. Boyle et al. 1977a; Sholkovitz 1978; Bale and Morris 1981; Wilke and Dayal 1982). This suggests that flocculation does not rapidly remove Fe from fjord waters, a situation observed by Mayer (1982) in the Gulf of Maine. Additional evidence for the importance of organics in retaining Fe in solution was obtained on August 5, 1981, the day of a heavy summer rain after an extended drought period. After the rain stopped, acid-soluble Fe concentration at station WA2B was $272 \pm 0\,\mu g \cdot L^{-1}$ (Fig. 2). The Fe concentrations at WA2 and WA1 were 251 ± 1 and $246 \pm 14\,\mu g \cdot L^{-1}$, respectively. A sample collected at SB1 on the following day had an acid-soluble Fe concentration of $164 \pm 2\,\mu g \cdot L^{-1}$. Clearly, a mechanism exists for transporting Fe throughout and perhaps beyond the fjord system.

Possible Consequences of Transport

The timing of exports of DOC, nutrients, and trace metals in the Wilson–Blossom system, as observed in the 1981–82 water years, may be optimum for perpetuating an ecosystem suitable for salmon survival. Higher levels of ammonia and phosphate are made available to intertidal areas at the same time that humic concentrations are the lowest. The presence of intensely colored, dissolved humics in the surface waters of Wilson Arm has been observed to severely reduce primary productivity relative to that in areas farther from freshwater influence (S. Sugai, unpublished data). It may restrict primary productivity in the intertidal region to an equal or greater extent. In August 1982, the surface carbon uptake rate was $4.32 \pm 0.24\,mg\,C \cdot L^{-1} \cdot h^{-1}$ at WA2 (Fig. 2) compared with $1.68 \pm 0.47\,mg\,C \cdot L^{-1} \cdot h^{-1}$ at SB1, a station with much higher seasonal carbon uptake. We suggest that this late summer productivity may be in part due to the river-supplied nutrients. Another consequence of the flow regime in the Wilson and Blossom rivers is that the concentration of Cu, a potentially toxic metal, is low during low discharge periods. Because the net effect of decreased river flow is an increase in water residence time, it is desirable that metals such as Cu be low, especially since humic compounds capable of making the Cu biologically unavailable are at a minimum during low-flow periods.

Acknowledgments

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Hypolimnetic Aeration and Zooplankton Distribution: A Possible Limitation to the Restoration of Cold-Water Fish Production

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Taggart, C. T. 1984. Hypolimnetic aeration and zooplankton distribution: a possible limitation to the restoration of cold-water fish production. Can. J. Fish. Aquat. Sci. 41: 191–198.

Hypolimnetic aeration of a 1.23-ha eutrophic kettle lake during two consecutive summers increased [O_2] to more than 4mg/L in the hypolimnion for extended periods. This improvement did not lead to the expected development of crustacean populations in the previously anoxic, zooplankton-deficient hypolimnion. The rotifer *Filinia longiseta* was the only zooplankter present, as isolated populations, in both the epilimnion and hypolimnion during summer. Eighty percent of the summer zooplankton community occurred exclusively in the epilimnion, and this was related to the development of an anoxic and toxic metalimnion that restricted migration from the epilimnion to the hypolimnion. Confinement of the zooplankton to the epilimnion coupled with predation by fathead minnows (*Pimephales promelas*) appeared to be responsible for the change in the zooplankton community from large cladocerans and copepods to smaller species. This study suggests that hypolimnetic aeration as a means of restoring or enhancing the production of cold-water fish may be thwarted by the development of a stable anoxic and toxic metalimnion that precludes the development of the zooplankton food resource.

L'aération hypolimnétique d'une marmite eutrophe d'une superficie de 1,23ha durant deux étés consécutifs eut pour effet d'augmenter [O_2] à plus de 4mg/L dans l'hypolimnion pendant de longues périodes. Cette amélioration n'a pas causé le développement anticipé des populations de crustacés dans un hypolimnion pauvre en zooplankton, précédemment anoxique. Le rotifère *Filinia longiseta* était le seul zooplancton présent, en populations isolées, à la fois dans l'épilimnion et l'hypolimnion en été. Quatre-vingt pour cent des communautés zooplanctoniques estivales ont été trouvées exclusivement dans l'épilimnion, et ceci a été attribué à la formation d'un métalimnion anoxique et toxique, imposant des restrictions à la migration de l'épilimnion vers l'hypolimnion. L'emprisonnement du zooplancton dans l'épilimnion, joint à la prédation par le tête-de-boule (*Pimephales promelas*), semble avoir été responsable du changement qui s'est produit dans la communauté zooplanctonique, depuis de gros cladocères et copépodes à des espèces plus petites. Cette étude donne à penser que l'aération hypolimnétique comme moyen de rétablir ou d'améliorer la production de poissons d'eau froide peut être limitée par la formation d'un métalimnion anoxique et toxique stable empêchant le développement de la ressource alimentaire zooplanctonique.

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Artificial techniques of lake restoration, including aeration, have met with varied success (Dunst et al. 1974; U.S. EPA 1980; Pastorok et al. 1981). The most common aeration method, destratification aeration, destroys the integrity of a stratified water column and produces warm (during summer) isothermal conditions unsuitable for cold-water fish. Hypolimnetic aeration, developed by Bernhardt (1967), permits the oxygenation of the hypolimnion without altering the natural thermal structure of the water column. A major goal of hypolimnetic aeration is to increase [O_2] in the hypolimnion of eutrophic lakes to the point at which cold-water fish can exist (Fast 1973, 1975, 1979; Overholtz et al. 1977; Keup 1979; Pastorok et al. 1981). Changes induced in water chemistry by hypolimnetic aeration are well documented (reviewed in Taggart and McQueen 1981), and to a lesser extent so are the effects on phytoplankton communities (Fast et al. 1973; Smith et al. 1975; Hickel 1978; Taggart 1980). Zooplankton are an important food for cold-water fish, yet there are no published studies on the effect of hypolimnetic aeration on zooplankton. This study was initiated to examine that effect on the vertical and temporal distribution of the zooplankton community in a small eutrophic lake.

Materials and Methods

Study Site

The study was carried out in Tory Lake, a 1.23 ha-eutrophic kettle lake situated 25 km north of Toronto, Ontario. The lake has a maximum depth of 10 m and an average depth of 4.5 m and has historically developed a strong thermocline between 2 and 4 m below the surface during summer. Additional details on morphometry are given in Taggart and McQueen (1981).

In May 1973, Tory Lake was anoxic below 0.3 m (Pope 1974), and during the summer of 1974, 90% of the zooplankton community was confined to the upper 2 m of the water column where [O_2] was 2 mg/L, decreasing to 0 mg/L at 5 m and below (Ellis and Tait 1981). Destratification aeration experiments by

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Ellis and Tait (1981) during the summers of 1975 and 1976 created isothermal conditions, a uniform O_2 profile that did not exceed 3 mg/L, and a uniform depth distribution of zooplankton down to 8 m.

In my study, the lake was subjected to hypolimnetic aeration from May to October 1978 and from May to November 1979. Full details of the aeration technique and the physical and chemical changes induced by aeration are given in Taggart and McQueen (1981, 1982); a relevant summary is provided below.

During periods of hypolimnetic aeration, the thermocline occurred between 2 and 6 m in 1978 and between 1 and 4 m in 1979. Accidental aerator leakage (pumping cold hypolimnetic water into the epilimnion) in early June 1978 caused partial destratification and subsequently a deeper thermocline when it restabilized by the end of June. The volume of water contained in the hypolimnion during summer stagnation was 7200 m^3 in 1978 and 17 700 m^3 in 1979. The epilimnion volume was 22 100 m^3 in 1978 and 11 600 m^3 in 1979. The metalimnion volume of 26 000 m^3 was equivalent in both years, but the zone was deeper and thicker in 1978. Aeration increased hypolimnetic $[O_2]$ to >2 mg/L between 15 May and 14 August and to >4 mg/L between 26 June and 15 July 1978 (Fig. 1a). In 1979, hypolimnetic $[O_2]$ exceeded 2 mg/L from 21 May to 14 July and exceeded 4 mg/L from 23 June to 6 July. Aeration was unable to satisfy hypolimnetic O_2 demand after mid-August 1978 and after mid-July 1979. From mid-June to late-September of both years the metalimnion was anoxic and potentially toxic due to concentrations of hydrogen sulfide, which periodically exceeded 5 mg/L (Fig. 1b).

Sampling Methods

Weekly (May–October) and biweekly (November–April) zooplankton collections were made between 10 May 1978 and 10 October 1979 at a station located 30 m northeast of the aerator, which was positioned over the deepest part of the lake (10 m). All samples were taken between 11:00 and 14:00 at discrete 1-m depth intervals ranging from surface to 7 m. A diaphragm pump (Parr, model 34600-00) connected to a weighted 2.5-cm (inside diameter) transparent vinylon tube was used for sampling. Sample volume was constant (50 ± 2.1 L) and pumping rate was 35 ± 0.1 L/min. Potential sample bias due to zooplankton avoidance and overdispersion was reduced by towing the intake tube through an arc of at least 15 m around the sampling station. Sampling studies with a similar system have shown that stationary sampling severely underestimates zooplankton abundance (D. J. McQueen, York University, Toronto, Ont., unpublished data). In winter, the sampling tube was lowered to the desired depth through a hole in the ice and was raised and lowered through a distance of 0.5 m at each sampling depth. The pump and hose were flushed between samples by pumping at least 20 L of water from the next depth to be sampled. Each sample was filtered through an 80-μm net and the concentrate preserved immediately in 5% formalin. Sample volume was later adjusted to 60–100 mL depending on the density of organisms in the concentrated sample.

To determine plankton density, four 1-mL vertical subsamples were withdrawn from each sample with a Hensen-Stempel pipette. All organisms in each subsample were counted using a Sedgewick-Rafter counting chamber and a Leitz SM-Lux compound microscope at 100 or 200× magnification. Representatives of three taxa (Cladocera, Copepoda, Rotatoria) were enumerated according to species, sex, and developmental stage (where possible). All counts were averaged and expressed as number per litre. Except when animals were scarce, the standard error was less than 10% of the density estimate. Although 29 species were identified from the limnetic zone, only 11 species and their subgroupings (total = 19) are considered here. Seventeen of the 18 species not considered were rotifers, which either did not form summer populations or occurred infrequently in the samples and at densities usually less than 5/L. Most were small soft-bodied rotifers, which are not sampled effectively by an 80-μm net (Likens and Gilbert 1970). The remaining species, *Bosmina coregoni*, occurred in only 5 of the 464 samples.

Analysis

To assess summer population densities, the data were divided according to three limnetic zones defined by the position of the thermocline during summer stagnation (i.e. 22 June–21 September 1978 and 4 May–27 September 1979). By these criteria, the epilimnion included sample data from 0, 1, 2, and 3 m in 1978 and 0, 1, and 2 m in 1979; the metalimnion included data from 4 and 5 m in 1978 and from 3 and 4 m in 1979; the hypolimnion included data from 6 and 7 m in 1978 and from 5, 6, and 7 m in 1979.

To determine whether significant differences in depth distribution of species groups among zones occurred during summer stagnation, the densities of each group at each depth were summed and the percent depth distribution was calculated. Individuals of a group had to be present at at least one depth for that date to be included in the group data set. Prior to analysis, these data were arc sine square root transformed to normalize their distributions. Data were grouped according to their respective limnetic zones. The mean of the transformed densities for each zone and group by sampling date was calculated. Analysis of variance was performed on the means of each group. The significance of differences among zonal means was tested using Duncan's multiple range test ($\alpha = 0.05$).

Results

Species Distribution

Cladocera

Daphnia pulex numbers increased rapidly in June 1978 (Fig. 2). At this time, hypolimnetic water was being inadvertently pumped into the epilimnion, which resulted in mixing of the water column to a near isothermal condition, and $[O_2]$ reached >2 mg/L to a depth of 7 m. Subsequently, *D. pulex* was present in all depth strata, but the majority of the population remained above 3 m. Reestablishment of the thermocline and the development of the anoxic metalimnion coincided with the collapse of the population. A small residual population remained in the hypolimnion until mid-August, when $[O_2]$ fell below 2 mg/L. In 1979, *D. pulex* was replaced by concurrent populations of *Daphnia parvula* (not shown) and *Diaphanasoma brachyurum* (Fig. 2). The latter species was also present in the second half of 1978 but at a relatively low density (Fig. 2). Virtually all *D. brachyurum* were restricted to the epilimnion in 1979. The depth distribution of *D. parvula* was similar to that of *D. brachyurum*.

Copepoda

Most copepods were restricted to the epilimnion during summer stagnation, especially the copepodids of the large predatory cyclopoid *Mesocyclops edax*, which was more numerous in 1978 than in 1979 (Fig. 3). The herbivorous calanoid *Diaptomus oregonensis* did not appear in the lake until late July

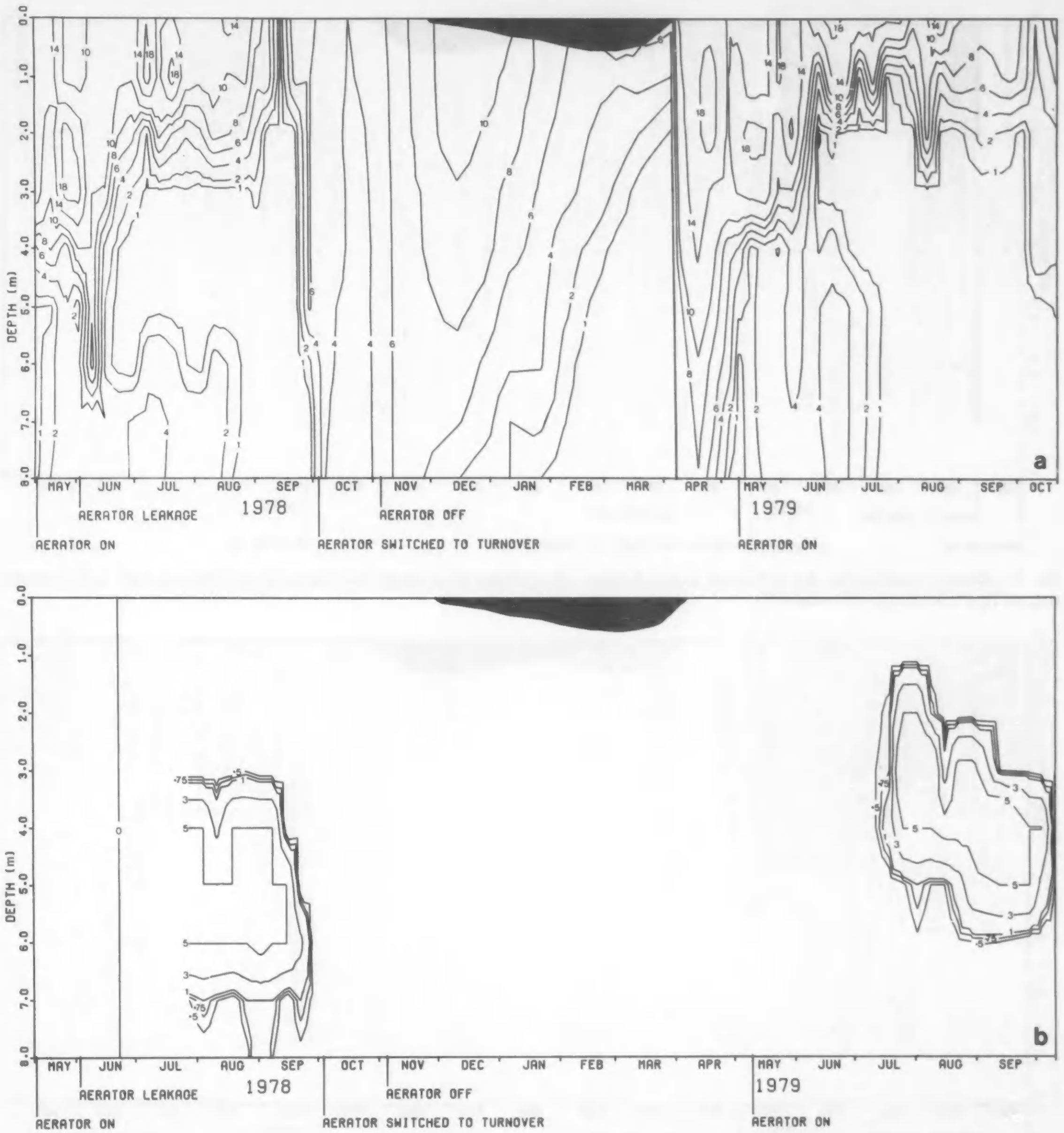

FIG. 1. (a) Dissolved O_2 isopleths (mg O_2/L) and (b) H_2S isopleths (mg H_2S/L) from Tory Lake in 1978 and 1979 at the zooplankton sampling station. H_2S data between 29 June and 20 July 1978 are unavailable. Ice cover is drawn to scale here and in subsequent figures.

1978, following the collapse of the adult population of *M. edax* (not shown). Adult *D. oregonensis* were present in the lake until the end of the study and were also restricted to the epilimnion during summer (Fig. 4). The small cyclopoid *Tropocyclops prasinus-mexicanus* became well established in June 1979 and was similarly restricted to the epilimnion. All copepod nauplii were confined to the epilimnion except during accidental destratification in June 1978 and at fall turnover (Fig. 5).

All copepod populations displayed progressive vertical restriction that coincided with the upward expansion of the anoxic metalimnion. This was particularly evident in June and July 1978 (Fig. 3 and 5) and in June and July 1979 (Fig. 3–5). A similar restriction was observed during winter for *D. oregonensis* (Fig. 4) when $[O_2]$ progressively decreased with time and depth. Depth distribution of all crustacean species expanded at spring and fall turnover.

Rotatoria

All but one rotifer species were virtually absent from the hypolimnion during summer stagnation. This was true even

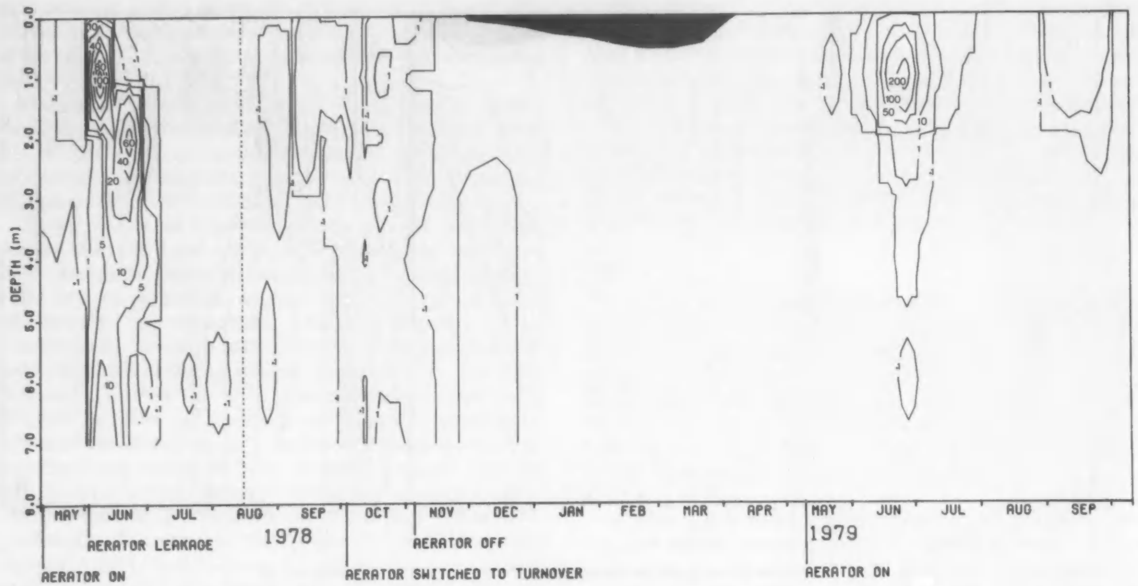

FIG. 2. Density isopleths (No./L) of *D. pulex* mature females (left of broken line) and *D. brachyurum* (right of broken line) in the limnetic zone of Tory Lake during 1978 and 1979.

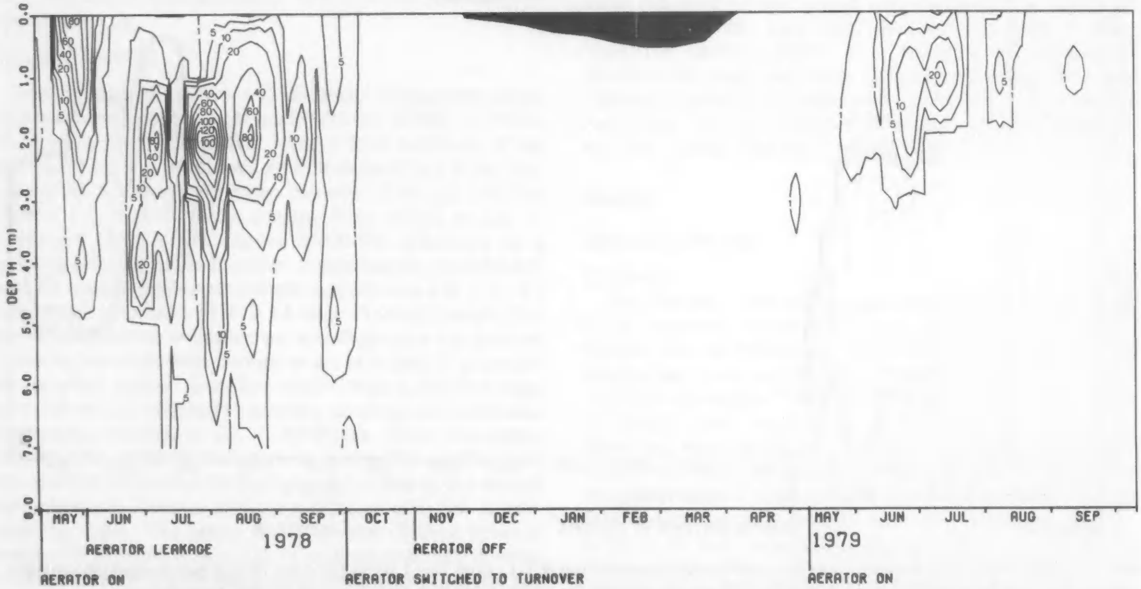

FIG. 3. Density isopleths (No./L) of *M. edax* copepodids in the limnetic zone of Tory Lake during 1978 and 1979.

when $[O_2]$ in the hypolimnion exceeded 4 mg/L. The sole exception was the rotifer *Filinia longiseta*, which was well established early in 1979 and became progressively more restricted to the epilimnion as metalimnetic $[O_2]$ decreased with time (Fig. 6). Immediately following spring turnover and the onset of aeration in 1979, the density of *F. longiseta* in the hypolimnion increased to a maximum of 2095/L by mid-July. This was followed by the development of a second but smaller population in the epilimnion. These two populations were separated by the metalimnion, where densities fell well below 25/L. The epilimnetic population persisted through to fall turnover, but the hypolimnetic population collapsed at the end of July when $[O_2]$ fell below 1 mg/L.

General Distribution Pattern

Eleven of 16 zooplankton groups displayed large differences ($P < 0.0001$) in their distribution among zones (Table 1). Of the

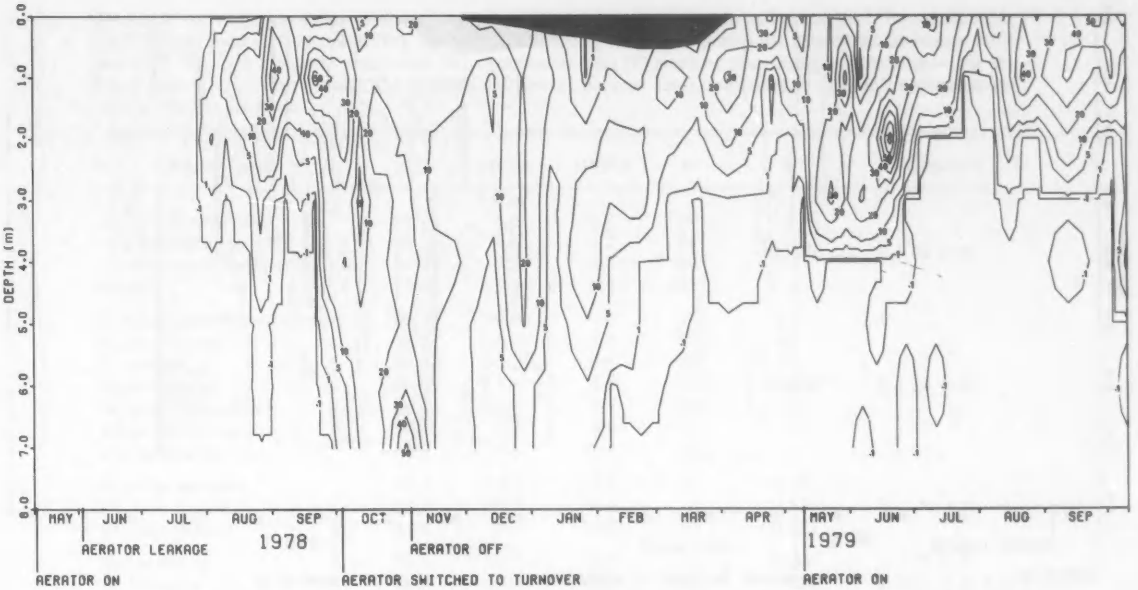

FIG. 4. Density isopleths (No./L) of *D. oregonensis* mature females in the limnetic zone of Tory Lake during 1978 and 1979.

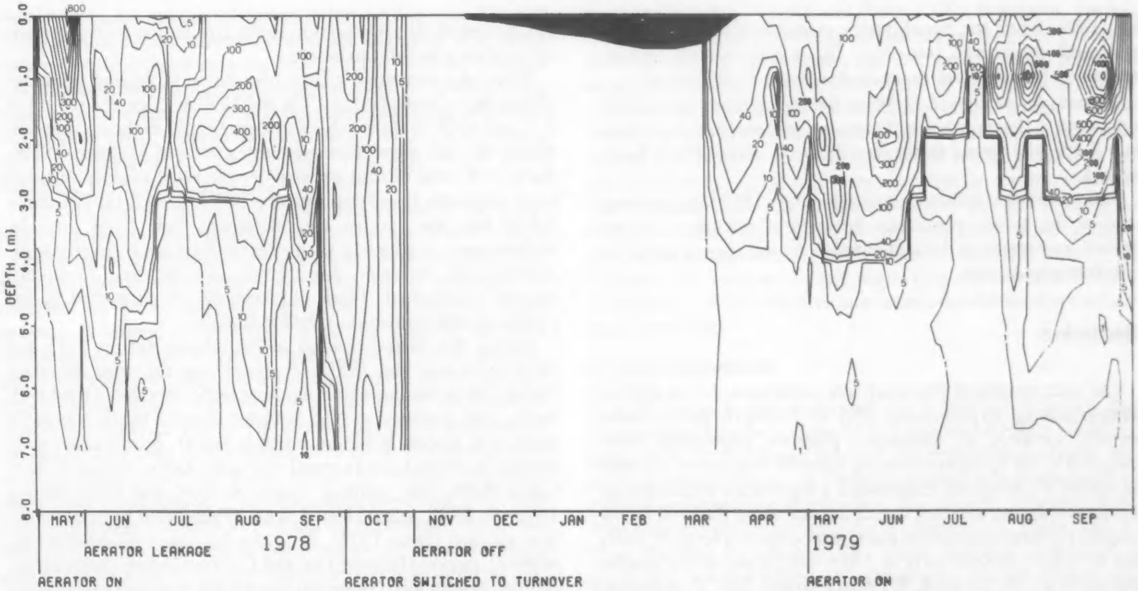

FIG. 5. Density isopleths (No./L) of copepod nauplii in the limnetic zone of Tory Lake during 1978 and 1979.

11, each of the 3 *D. oregonensis* groups and all copepod nauplii had an average of 93.4% of their total density concentrated in the epilimnion. The metalimnion contained an average 5.9% of the populations, and this was in each case significantly greater than the average of 0.7% found in the hypolimnion. Greater than 90% of the remaining seven groups (containing representatives of cladocerans, copepods, and rotifers) were also concentrated in the epilimnion. An average of 62% of *D. pulex* females and neonates and female *M. edax* were found in the epilimnion. However, these three groups showed no significant stratifications with depth.

Anomalous distributions of *Polyarthra* sp. and *F. longiseta* were apparent. *Polyarthra* was significantly more concentrated in the metalimnion, but it should be noted that this species was not observed after the end of June 1979 when the metalimnion became anoxic. *Filinia longiseta* was concentrated in the epilimnion and the hypolimnion, with only 13% of the population found in the metalimnion. Between 13 June and 25

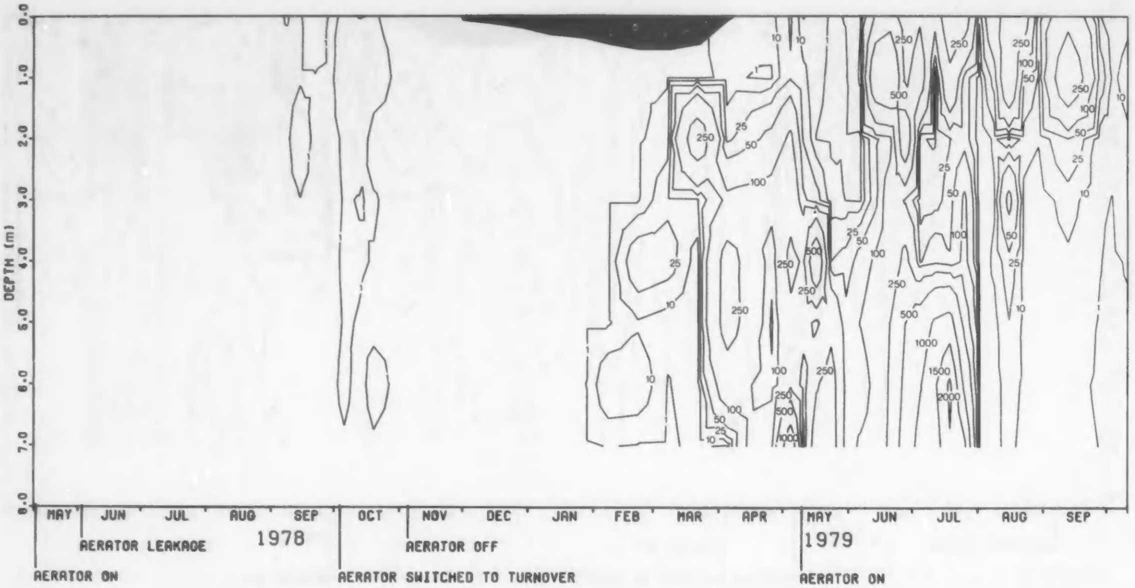

FIG. 6. Density isopleths (No./L) of *F. longiseta* in the limnetic zone of Tory Lake during 1978 and 1979.

July 1979, when the hypolimnetic population of *F. longiseta* was well developed (see Fig. 6), a significantly greater proportion (65.1%) was concentrated in the hypolimnion.

Overall, an average of 78.8% of the zooplankton community was found in the epilimnion during summer stagnation and less than 9.4% was found in the hypolimnion while it was being aerated.

Diel sampling conducted during 4–5 July 1979 indicated that none of the groups penetrated below 1 m and there was no upward movement to the metalimnion by the hypolimnetic *F. longiseta* population.

Discussion

The main results of this study are as follows: (1) in spite of aerator-induced hypolimnetic [O_2] to >4 mg/L for extended periods, virtually all crustacean plankton populations were restricted to the epilimnion during summer stagnation; (2) only the rotifer *F. longiseta* established a significant hypolimnetic population during aeration that collapsed when [O_2] fell below 1 mg/L; (3) large cladoceran and copepod species (e.g. *D. pulex* and *M. edax*) present early in 1978 were replaced by smaller species (e.g. *D. parvula*, *D. brachyurum*, and *T. prasinus-mexicanus*). The implication here is that researchers and managers involved with lake restoration and hypolimnetic aeration who have the declared intention of enhancing or restoring cold-water fish production should consider carefully the trophic, thermal, and chemical structure of their lake during summer stagnation prior to making a research or managerial commitment.

The restriction of zooplankton populations to the epilimnion and the change in the species composition appear to be linked and to result from a migration barrier imposed on the community by the presence of an anoxic and toxic metalimnion. Restriction of the zooplankton to the epilimnion increases their vulnerability to fish predation.

Tory Lake contained a large population of fathead minnows (*Pimephales promelas*) in 1978 and 1979 at a density of 1.69 ± 0.11 and 1.46 ± 0.08 fish/m^3, respectively, in the epilimnion, where the fish were also naturally confined (Taggart 1980). These fish feed almost exclusively on large cladocerans and large copepods (Held and Peterka 1974). Lynch (1979) established that the species can eliminate their large prey by mid-summer, at which time smaller cladocerans and rotifers (*D. parvula*, *D. ambigua*, *Brachionus*, *Filinia*, and *Keratella*) become established. These observations are supported by the results of destratification aeration studies.

During the destratification of Tory Lake during 1975 and 1976 (Ellis and Tait 1981), *D. pulex* was the most abundant cladoceran in the limnetic zone, was uniformly distributed with depth, and persisted at [O_2] between 2 and 3 mg/L. *Daphnia pulex* was absent, while *D. parvula* and *D. brachyurum* were present in Heart Lake (a small eutrophic kettle similar to Tory Lake) during the "control" years of 1968 and 1969 (Haney 1970). In 1976, when Heart Lake was subjected to destratification aeration (Strus 1976), *D. pulex* became well established, while *D. parvula* became rare and *D. brachyurum* disappeared. Similar results were observed among the copepod populations when *Cyclops bicuspidatus thomasi* was replaced by *M. edax* and to a lesser extent by *T. prasinus-mexicanus* following destratification aeration. Destratification aeration in Lake Calhoun also resulted in *D. pulex* establishing a limnetic population (Shapiro et al. 1975). The above authors suggested that the success of populations of large zooplankton in destratified lakes results from the increased ability of larger individuals to avoid fish predators through prey dilution and their inhabiting deeper waters. Both factors result from the expanded limnetic habitats created by destratification aeration.

The metalimnion may not be a barrier to vertical migration if

TABLE 1. Average percent population density of each zooplankton group in the epilimnion (EPI, E), metalimnion (META, M), and hypolimnion (HYPO, H) of Tory Lake during summer stagnation and hypolimnic aeration in 1978 and 1979. For each group the sample size (*N*), significance level (*P*) resulting from analysis of variance on the arc sine square root, average density, and the density difference between zones determined by Duncan's multiple range test ($\alpha = 0.05$) are given.

Species group	EPI	META	HYPO	*N*	*P*	Duncan's
D. oregonensis males	93.7	5.6	0.7	69	<0.0001	E ≠ M ≠ H
D. oregonensis females	92.3	7.6	0.2	84		
D. oregonensis copepodids	94.0	5.2	0.7	84		
Nauplii	93.6	5.3	1.2	102		
T. prasinus mexicanus females	100.0	0.0	0.0	39	<0.0001	E ≠ M = H
D. brachyurum	95.2	1.7	3.1	36		
D. parvula	94.2	5.2	0.6	15		
Brachionus sp.	88.3	7.8	3.9	51		
M. edax copepodids	88.2	6.5	5.3	90		
Keratella cochlearis	84.7	8.4	6.9	84		
Asplanchna sp.	84.7	4.5	10.8	30		
D. pulex neonates	68.4	13.7	17.9	9	<0.25	E = M = H
D. pulex females	53.3	36.6	10.1	6	<0.53	
M. edax females	64.9	10.2	24.9	90	<0.22	
Polyarthra sp.	24.3	58.0	17.7	24	<0.004	E = H ≠ M
F. longiseta	40.3	12.9	46.8	60	<0.026	E = M ≠ M = H
F. longiseta (peak population)	28.6	6.4	65.1	21	<0.0002	E = M ≠ H

the resident zooplankton are nonmigratory. All species found in Tory Lake, and their close relatives, are migratory in systems where chemical conditions are less extreme. Where chemical conditions become suboptimal, the animals move upward in the water column where preferred conditions exist (Langford 1938; Hutchinson 1967; George and Fernando 1969, 1970; Haney 1973; Hoffman 1975, 1977, 1982; Fairchild et al. 1977; Threlkeld 1979; Burns and Mitchell 1980).

The fact that *F. longiseta* became established in the hypolimnion indicates that hypolimnetic aeration can be effective in creating suitable conditions for the establishment of hypolimnetic zooplankton populations. However, as the treatment has no effect on the metalimnion, the populations tend to remain isolated. A similar but naturally occurring situation has been documented in Lake Johnson, New Zealand, where concentrated zooplankton populations were isolated in the oxygenated hypolimnion, which was overlain by an anoxic metalimnion (Burns and Mitchell 1980). The authors suggested that some of the populations may have resulted from either lateral migration of individuals from the shore region or vertical migration through the metalimnion. The information presented in the Tory Lake study does not support this second hypothesis. Burns and Mitchell (1980) also assumed that some species became trapped in the hypolimnion by the developing anoxic metalimnion. This is consistent with my view of the establishment of *F. longiseta* in the hypolimnion of Tory Lake. It is possible that the epilimnetic population that developed later resulted from pumping individuals from the hypolimnion when sampling and releasing them into the epilimnion. The same technique used in reverse may be suitable for stocking epilimnetic zooplankton into the hypolimnion, but the persistence of stocked populations will be poor if vertical migration to the productive epilimnion is impeded by the anoxic and toxic metalimnion.

The natural development of metalimnetic O_2 minima in thermally stratified lakes is believed to result from zooplankton and algal biomass settling from the epilimnion and decaying in the metalimnion (Mitchell and Burns 1979). Ironically, the use of hypolimnetic aeration in lakes that are prone to the development of metalimnetic minima and that are frequently regarded as prime candidates for aeration (Ohle 1974; Fast et al. 1975; Wirth et al. 1975) may be misdirected, particularly if the intention is to create improved chemical conditions for cold-water fish. Suitable chemical conditions can be created in the hypolimnion by hypolimnetic aeration, but the results presented here indicate that the development of suitable biological conditions may be limited by the presence of an anoxic, H_2S-rich metlimnion. A metalimnetic minimum cannot be corrected by aeration without destroying thermal stratification (Wirth et al. 1975), which in turn creates conditions that exclude cold-water fish.

Acknowledgments

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POSTSCRIPT ADDED IN PROOF: Subsequent to this paper being accepted for publication I became aware of work by K. I. Ashley (1983. Hypolimnetic aeration and functional components of the lake ecosystem: phytoplankton and zooplankton effects, p. 31–40. *In* J. Taggart and L. Moore [ed.] Lake restoration, protection, and management. Proc. Second Annu. Conf. North Am. Lake Manage. Soc., 26–29 Oct. 1982, Vancouver, B.C. U.S.

EPA 440/5-83-001: 327 p.). The zooplankton in Ashley's partitioned lake (hypolimnetic aeration experiment and control sides) did not respond as expected to the aeration treatment. The vertical distribution of zooplankton was not significantly different between the control and experimental sides. This was attributed to the fact that the control side was partially aerobic during the experiment, thereby negating any experimental difference in hypolimnion oxygen concentration against which zooplankton response could be assessed. Ashley's findings are in support of those presented here, although he suggests that long-term aeration may result in an expanded vertical range of zooplankton.

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NOTES

Parr–Smolt Transformation of Atlantic Salmon (*Salmo salar*): Activities of Two Respiratory Enzymes and Concentrations of Mitochondria in the Liver

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Hatchery-reared parr and smolts of Atlantic salmon (*Salmo salar*) derived from spawners of the Big Salmon, Saint John, and Penobscot rivers were analyzed for activity of two respiratory chain enzymes in liver. Cytochrome *c* oxidase activity was about 15-fold greater in enzyme units than succinate dehydrogenase in all three experimental groups. Smolt sample means for cytochrome *c* oxidase and succinate dehydrogenase in Big Salmon and Saint John fish were significantly greater than those of parr. Measurements in Big Salmon fish, which had the greatest parr–smolt difference in cytochrome *c* oxidase units and condition factor, demonstrated a significantly greater smolt sample mean for liver mitochondria concentrations. The results are discussed primarily in relation to the possible role of thyroid hormone in causing a greater potential for aerobic energy generation in liver during smoltification and the utilization of lipid as an energy resource.

Les auteurs ont analysé l'activité de deux enzymes de la chaîne respiratoire hépatique chez des tacons et des saumoneaux Atlantiques (*Salmo salar*) d'élevage engendrés par des reproducteurs des rivières Big Salmon, Saint-Jean et Penobscot. Chez les trois groupes expérimentaux, l'activité de la cytochrome *c* oxidase était environ quinze fois plus élevée que celle de la succino-déhydrase. Le niveau moyen de la cytochrome *c* oxidase et de la succino-déhydrase chez les échantillons de saumoneaux des rivières Big Salmon et Saint-Jean était sensiblement plus élevé que chez les tacons. Chez les poissons de la Big Salmon, où existait la plus grande différence du nombre d'unités de cytochrome *c* et du facteur de condition entre les saumoneaux et les tacons, les résultats ont révélé des concentrations moyennes de mitochondries hépatiques sensiblement plus élevées chez les saumoneaux. Les résultats sont surtout présentés, d'une part, en relation au rôle possible de l'hormone thyroïdienne dans le potentiel élevé de production d'énergie aérobie dans le foie au cours de la smoltification et, d'autre part, en relation à l'utilisation des lipides comme source d'énergie.

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Prior to entering the ocean, Atlantic salmon (*Salmo salar*) undergo smoltification which preadapts them for life in the sea. This dramatic transformation is an energy-demanding process involving a variety of morphological, behavioral, and physiological changes (Hoar 1976; Folmar and Dickhoff 1980; Wedemeyer et al. 1980). Our study considers the physiological processes with particular reference to metabolism and energy production.

Changes in energy metabolism during smoltification appear to be the consequence of the activation of endocrine glands. Increased thyroid cell activity occurs in Atlantic salmon during smoltification (Hoar 1939a); smolts have elevated thyroid hormone (T_3 and T_4) levels (Dickhoff et al. 1979), which are associated with aerobic energy production. Changes occur in the apparent activity of growth hormone-producing cells in the pituitary (Olivereau 1954; Komourdjian et al. 1976a, 1976b); a period of rapid growth accompanies smoltification (Elson 1957; Parry 1958; Saunders and Henderson 1970). Administration of growth hormone to Atlantic salmon parr results in increased growth rate, decreased condition factor, and increased salinity tolerance (Komourdjian et al. 1976a). The pituitary–interrenal axis is activated during smoltification (Fontaine and Olivereau 1959) and tissue water content increases (Houston and Threadgold 1963). Decreases in tissue chloride (Fontaine 1951) and sodium (Houston 1960) develop in association with increased hypoosmotic regulatory capacity in smolts. The activity of Keys–Willmer (chloride) secreting cells of the gills increases during smoltification (Van Dyck 1966) as does gill microsomal Na$^+$K$^+$-ATPase activity (McCartney 1976; Saunders and Henderson 1978; Johnston and Saunders 1981).

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Metabolic differences observed in smolts are reduced liver glycogen and elevated blood glucose levels (Wendt and Saunders 1973), increased ammonia excretion (A. J. Wiggs, University of New Brunswick, unpublished data), and decreased total body lipid content (Hoar 1939b; Komourdjian et al. 1976a; Farmer et al. 1978; Saunders and Henderson 1978). Atlantic salmon smolts consume greater amounts of oxygen than parr (Power 1959; Withey and Saunders 1973), which may indicate greater reliance on aerobic energy generating mechanisms to fuel smoltification. The marked decrease in total body lipid levels in smolts, compared with parr, suggests that lipid represents a major energy resource during smoltification. If this is so, then increased respiratory chain function would be expected because the metabolic pathway of lipid oxidation is linked to aerobic energy generation in mitochondria. As an experimental approach to investigate this possibility, cytochrome *c* oxidase (CCO, ferrocytochrome *c*:oxygen oxidoreductase, EC 1.9.3.1) activities and mitochondria concentrations were measured in livers of parr and smolts, as liver occupies a central role in the intermediary metabolism of vertebrates. CCO, the terminal oxidase of the mitochondrial respiratory chain, reacts directly with oxygen, and its activity is a measure of the potential of the respiratory chain for aerobic function. Succinate dehydrogenase (SDH, succinate:acceptor oxidoreductase, EC 1.3.99.1) was also measured as a basis for comparison.

Materials and Methods

Yearling (1+) parr and smolts derived from the Big Salmon River and Saint John River spawners were reared at the North American Salmon Research Center (NASRC) in St. Andrews, New Brunswick. At the NASRC, full sib family groups were incubated and reared separately under elevated temperature conditions (6°C for incubation and 10–14°C for early feeding) to accelerate hatching and early growth. Thereafter, temperature and photoperiod followed the natural seasonal cycles. In June, the underyearling (0+) parr were combined by strain in circular outdoor rearing tanks (8 m in diameter) where they remained until used for experimental purposes the following year. The fish were fed Sterling Silver Cup feed to satiation three to four times daily during spring, summer, and fall and once daily in winter.

At the Green Lake National Fish Hatchery (GLNFH), Penobscot underyearling fish were grown in circular fiberglass tanks 1.83 m in diameter at ambient water temperatures, under a natural photoperiod with no direct sunlight, and fed BIO-DIET from Oregon. In late spring, they were transferred to outdoor rearing tanks where they remained until the following year.

Fish from NASRC and GLNFH were collected by random sampling on June 26 and July 5, respectively, and killed for measurement of fork length (millimetres), body weight (grams), and condition factor (K) computed as body weight/(fork length)^3 × 100. Livers were removed, rinsed in potassium phosphate buffer (0.05 mol/L, pH 7.5), blotted, weighed (liver weight in 0.01 g), and transferred with chilled buffer to beakers in an ice container. The livers were minced with scissors, and then homogenized with the buffer in TenBroeck tissue grinders (glass pestle) chilled in ice to prepare 25% homogenates (w/v).

CCO activity was assayed by the method of Wharton and Tzagoloff (1967). The rate of oxidation of ferrocytochrome *c* (horse heart type III, Sigma Chemical Co., St. Louis, MO) was assayed by a decrease in absorbance at 550 nm. Spectrophotometric analyses were conducted with a Bausch & Lomb double-beam Spectronic 210 UV. The final reaction mixture contained 20 μmol of potassium phosphate buffer (pH 7.0), 50 μL of the liver homogenate (1:10 dilution), 1.4 mg of ferrocytochrome *c*, and deionized–distilled water to 2.0 mL. Ferrocytochrome *c* in the blank was oxidized by the addition of 2 μmol of potassium ferricyanide. Initial reaction rates were taken for calculation of enzyme units. Enzyme activities are expressed as nanokatals of substrate oxidized at 25°C. Katal (kat) is the amount of enzyme activity that converts 1 mol substrate/s.

For comparative purposes a noncytochrome respiratory chain enzyme, the flavoprotein SDH, was assayed in liver homogenates by the method of Kramar (1967). The SDH reaction mixture contained 150 μmol of potassium phosphate buffer (pH 7.5), 10 μmol of sodium azide, 1 μmol of 2-*p*-iodo-3-nitro-5-phenyltetrazolium chloride (INT, Sigma Chemical Co., St. Louis, MO), 20 μmol of sodium succinate, and an aliquot of the liver homogenate in a final volume of 2.0 mL. INT reduction was followed at 500 nm for 5 min.

Mitochondria concentrations of liver homogenates were determined by a modification (Blake 1977) of the method of Allard et al. (1952). Prior to counting, mitochondria were stained for SDH activity by coupling the oxidation of succinate to the reduction of INT, using the same reaction mixture as for the assay of SDH activity, except that menadione was omitted. After about 20 min of staining, the reaction mixture was diluted fivefold in 0.25 mol sucrose/L. An aliquot of the diluted suspension was pipetted with a Hamilton syringe to the edge of the cover glass of a Petroff-Hauser bacteria counter and allowed to settle for at least 15 min. The field was examined by light microscopy, using a Leitz Labourlux at 1425× magnification with oil immersion. Twenty squares (prisms) were counted per field per sample in duplicate. The results were calculated as 10^{10} mitochondria/g liver.

Results

There was a trend for greater respiratory chain enzyme activity in livers of smolts than in parr (Table 1). In general, CCO enzyme units were about 15-fold greater than SDH enzyme units for both parr and smolts in all three experimental groups. The greatest parr–smolt difference in CCO activity was observed in fish of the Big Salmon River strain. The CCO sample mean of the Big Salmon River smolts was significantly greater ($P < 0.001$) than that of the parr with a 74.1 enzyme unit difference compared with 43.0 ($P < 0.01$) and 17.0 (not significant) for the Saint John and Penobscot fish, respectively. Analyses of the liver mitochondria concentrations in Big Salmon River fish also demonstrated greater numbers in smolts than in parr. The sample mean for mitochondria concentrations in the Big Salmon River smolts ($N = 5$) was $4.3 \pm 0.5 \times 10^{10}$/g liver, which is significantly greater ($P < 0.02$) than for the parr ($N = 5$), $2.6 \pm 0.2 \times 10^{10}$. A comparison of the morphological properties of the fish used in this study (Table 2) demonstrated that, whereas the sample means for fork length, body weight, and liver weight were statistically greater in smolts than in parr

TABLE 1. Enzyme units of CCO and SDH in parr and smolt livers. Results are presented as the sample mean (standard error in parentheses). Enzyme units were calculated as nkat/g liver. Tests for statistical levels of significance were determined by the two-sample Student *t* distribution. N = number of parr/smolts in the samples.

	Strain					
Enzyme	Big Salmon ($N = 6/6$)	P	Saint John ($N = 6/6$)	P	Penobscot ($N = 5/6$)	P
CCO						
Smolts	208.6 (2.3)	<0.001	185.8 (9.3)	<0.001	135.2 (5.4)	NS
Parr	134.5 (8.9)		142.8 (8.2)		119.2 (14.3)	
SDH						
Smolts	12.6 (0.6)	<0.002	12.9 (0.8)	<0.02	7.4 (0.5)	NS
Parr	8.8 (0.5)		9.6 (0.7)		8.5 (0.7)	

TABLE 2. Morphological properties of Big Salmon, Saint John, and Penobscot 1+ parr and smolts. Results are presented as the sample mean (standard error in parentheses). Tests for statistical levels of significance were determined by the two-sample Student *t* distribution. N = number of parr/smolts in the samples.

	Strain					
Parameter	Big Salmon ($N = 6/6$)	P	Saint John ($N = 6/6$)	P	Penobscot ($N = 5/6$)	P
Fork length (mm)						
Smolts	178 (1.0)	<0.001	160 (5.0)	<0.001	165 (7.0)	<0.001
Parr	123 (4.0)		113 (3.0)		117 (3.0)	
Body weight (g)						
Smolts	56.42 (2.89)	<0.001	43.86 (3.51)	<0.001	56.12 (6.87)	<0.002
Parr	22.79 (2.17)		16.18 (1.98)		19.41 (7.22)	
Condition factor						
Smolts	0.99 (0.02)	<0.001	1.06 (0.03)	NS	1.21 (0.02)	NS
Parr	1.19 (0.02)		1.10 (0.03)		1.20 (0.03)	
Liver weight (g)						
Smolts	0.60 (0.04)	<0.001	0.45 (0.03)	<0.001	0.53 (0.09)	<0.05
Parr	0.35 (0.03)		0.20 (0.01)		0.28 (0.01)	

for all three strains, only the Big Salmon River smolts had a significantly lower condition factor than the parr.

Discussion

The greater activity of CCO compared with SDH in liver mitochondria of juvenile Atlantic salmon is consistent with the known structure–function relationships of these two inner-membrane enzymes. CCO not only functions enzymatically as the terminal oxidase for all respiratory chain activity but also acts as an important structural component of the inner-membrane cristae network during mitochondrial biogenesis (Saltzgaber et al. 1977) and is thought to be encoded by both nuclear and cytoplasmic genomes in various species varying in complexity from yeast to mammals. Atlantic salmon are known to prefer cold, well-oxygenated freshwater and to be extremely active and vigorous swimmers. It is logical to assume, therefore, that CCO function may represent a critical process in the cellular respiratory mechanisms of aerobic energy generation in this species. The lower SDH activity in liver mitochondria of 1+ parr and smolts may reflect less utilization of the metabolic pathway linking the tricarboxylic cycle to the mitochondrial respiratory chain by succinate oxidation. The reduced liver glycogen levels of smolts compared with parr were accompanied by elevated blood glucose levels (Wendt and Saunders 1973), indicating carbohydrate mobilization to peripheral tissues for glycolysis. In liver, aerobic energy generation may involve greater utilization of other metabolites such as fatty acids. Mitochondrial enzymes of fatty acid oxidation (e.g. fatty acid:CoA ligase AMP) should be assayed in various tissues of Atlantic salmon parr and smolt.

Variations in CCO enzyme unit difference among the three experimental groups probably do not reflect intrinsic strain differences in the regulation of liver CCO during smoltification. Although interesting characteristics of Big Salmon River fish have been reported, such as the high incidence of grilse (Schaffer and Elson 1975) and repeat spawners (Ducharme 1969) and precocious maturation among male parr (Saunders and Sreedharan 1977), the differences in CCO activity observed in this study were more likely owing to variation in the time of smoltification. Fish reared at the GLNFH may have smolted earlier than those reared at the NASRC. Reversion of Penobscot smolts to a parr-like condition could account for the lower CCO and SDH activities in these "smolts." Although our smolts were sampled in late June and early July, 4–6 wk later than they would have emigrated to sea had they been given the opportunity, they still retained smolt growth patterns and other smolt characteristics such as silvery scales and dark fin margins. Saunders and Henderson (1969) demonstrated that the growth of smolts and postsmolts retained in freshwater was as great or greater than in those reared at various salinities up to 30‰.

Hormonal inducers of protein synthesis must be maintained above a threshold level concentration to promote continued activity of genetic expression (Tata 1968). The greater activity of CCO in smolt livers may be due to the action of thyroid hormone. Hoar (1939a) reported increased activity of thyroid gland cells of Atlantic salmon at the time of smoltification. Dickhoff et al. (1978) demonstrated a plasma thyroxin (T_4) surge during smoltification of coho salmon (*Oncorhynchus kisutch*) in which T_4 concentrations changed from basal levels of 14–18 ng/mL, peaking at 65–91 ng/mL in midspring, and subsequently returning to basal levels before summer solstice. Massey and Smith (1968) reported that the administration of T_4 to brown trout (*Salmo trutta*) caused elevated specific activity of oxidative enzyme systems for succinate, glutamate, and β-hydroxybutyrate in liver mitochondrial preparations. Le Ray et al. (1970) reported that the administration of T_4 to mullet (*Mugil auratus* L.) increased the activity of liver CCO. T_4 is also known to stimulate lipid metabolism in salmonids; Barrington et al. (1961) demonstrated that rainbow trout (*Salmo gairdneri*) treated with T_4 had less abdominal fat. Narayansingh and Eales (1975) reported decreased hepatic and visceral lipid reserves in brook trout (*Salvelinus fontinalis*) after T_4 treatment.

The greater liver CCO activity in Atlantic salmon smolts compared with parr could be owing either to quantitative changes in enzyme function or to enzyme concentration. Administration of thyroid hormone to certain endotherms has been reported to cause an increase in the concentration of mitochondria. Wooten and Cascarano (1980) reported that the administration of T_4 to rats caused a significant stimulation of total body respiration and succinate and α-glycerophosphate dehydrogenase activities of liver and an increase in mitochondria number and mass in liver. Elevated α-glycerophosphate dehydrogenase activity and mitochondria concentrations occurred in livers of mice after the administration of L-triiodothyronine (Blake and Hall 1976). CCO activity was also increased in livers of treated mice. To investigate the possibility of elevated liver mitochondrial concentrations in Atlantic salmon smolts, we analyzed samples from the Big Salmon River fish, as the parr–smolt difference in liver CCO activity was greater in this than in the other strains studied. If the number of mitochondria in livers of Big Salmon River fish had remained constant during the parr–smolt transformation, then the mitochondria concentrations would have been about 1.5×10^{10}/g liver. Instead, the liver mitochondria concentrations in Big Salmon River smolts were about 1.65 greater than those of the parr, showing that a marked change in liver mitochondria concentrations occurred during the parr–smolt transformation. The elevated mitochondria concentrations and CCO activities of Big Salmon smolts can be taken as evidence of an increased potential for aerobic energy generation in liver. This potential may be transitory, however, occurring only during smoltification to provide the additional energy required for transformation. Comparisons should be made of smolts maintained in both fresh water and salt water to determine whether liver CCO activity and mitochondrial concentrations return to parr levels. Do Atlantic salmon smolts growing in salt water maintain an elevated potential for aerobic energy generation in liver?

The increased liver CCO activity and mitochondrial concentrations during smoltification raise interesting speculations of phylogenetic significance about this control mechanism. Perhaps wholly freshwater species such as *Salvelinus namaycush* can not increase their aerobic energy generation potential by thyroid hormone. It would be of interest to know more about the species variation in thyroid hormone induction of aerobic energy generation in Salmonidae and in totally marine species as well.

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Female Size and Nest Depth in Coho Salmon (*Oncorhynchus kisutch*)

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van den Berghe, E. P., and M. R. Gross. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 41: 204–206.

Nest depth was strongly correlated with female size in coho salmon (*Oncorhynchus kisutch*). Since nests of different-sized females are at different depths, they are differentially vulnerable to destruction by floods and to other females competing for the same nest sites.

La profondeur du nid était en étroite corrélation avec la taille de la femelle du saumon coho (*Oncorhynchus kisutch*). Parce que les nids de femelles de tailles différentes se trouvent à des profondeurs variables, leur vulnérabilité varie face à la destruction par les inondations ou à la compétition des autres femelles pour les mêmes sites de reproduction.

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Female salmonids spawn into nests they construct in stream beds. Nests are excavated using a series of lateral body flexures, which produce a vortex, lifting gravel to be carried downstream by the current. After egg deposition, the female moves upstream and with the same digging motion, covers the nest (Foerster 1968; McCart 1967; Tautz and Groot 1975). The function of egg burial is to increase brood survivorship by decreasing predation (Reed 1967; Stuart 1953, cited in Jones 1959), mechanical damage, and agitation, which is lethal during critical periods of brood development (Smirnov 1955). The relationship between substrate quality and brood survivorship has been well studied (Coble 1961; Dill and Northcote 1970; and others). However, an important but less well studied factor for brood survivorship is nest depth. Increased depth will afford greater protection from mechanical damage and exposure when gravel is shifted by floods and when nests are superimposed by competing females. Superimposition, or reuse of a nest site by later-spawning females, is a common phenomenon in salmonids and is responsible for considerable brood loss (McNeil 1962; Schroder 1973; and others).

Studies reporting nest depth give depths at which investigators encountered eggs in the course of excavating redds (e.g. Burner 1951; Hawke 1978). Such data may be relatively inaccurate due to the frequent and often extensive gravel shifts associated with fluctuating water levels. McNeil (1962), for instance, showed gravel shifts in one season to exceed 25 cm at one third of his sites. Shifts of such magnitude would destroy many of the shallower nests, removing them from the sample. A further important shortcoming of existing nest depth data is the lack of information on female size. Larger females make deeper nests in brown trout (*Salmo trutta*) (Ottaway et al. 1981) and possibly in salmon (Jones 1959; Major and Craddock 1962; Ricker 1972). If so, the destructive effect of nest reuse and flooding will differentially affect females of different size; this would have important management implications for salmonid populations. Therefore, we measured nest depths when coho salmon (*Oncorhynchus kisutch*) of known body size spawned.

Methods

We collected data on a small wild population of spawning coho salmon native to a tributary of Deer Creek, 1.8 km west of Index, Snohomish Cty, WA. During November–January of 1981–82 and 1982–83, all fish were caught at a weir near the mouth of the stream. The fish were measured to the nearest half centimetre (fork length), sexed, and tagged using color-coded Petersen disk tags (Floy Tag Co., Seattle, WA). Tagging permitted subsequent recognition of individual fish. All fish were released above the weir to spawn naturally.

Substrate samples, each consisting of about 4 kg of material, were collected with a shovel at 2-m intervals in midstream along the entire spawning ground. This provided samples to a depth of 25 cm, which we considered to be representative of that affected by the fishes' digging. Examination of the stream substrate showed no significant layering to that depth (analysis of six samples taken at 0–5, 10–15, and 20–25 cm, MANOVA (Nie et al. 1975) $P = 0.699$, 0.908, 0.821, and 0.560 for comparisons between depths). All gravel in the stream was of a smooth, rounded texture. Samples were analyzed in the laboratory and fredle indices were calculated (Lotspeich and Everest 1981). Nest sites were characterized by superimposing the fredle scores on a grid map locating the nests. To minimize the effects of spacial heterogeneity in gravel, only those nests with centers within 50 cm of a gravel sampling locality were used.

Nest depth was defined as the maximum depth that a female excavated her nest. This was calculated as the distance from the top of the water column to the deepest place in the nest, minus the distance from the top of the water column to the top of undisturbed substrate around the nest. A series of nest measurements were taken preceding and following the spawning. The greatest depth is used here as the final nest depth. Measurements were made from shore using a meterstick attached at right angles to a pole; this minimized spawning disturbance. Records were kept, until death, on 83 of 160 females that spawned in the stream. Of these, measurements were obtained during daylight hours for nests of 42 females. Because of the often unpredictable moment of egg release, observation periods on individual fish were of variable duration. Although the females could not be observed at night, the locations of their nests and the identity of the females were rarely in doubt, since digging was often initiated during the daytime and covering frequently continued long after sunrise. Disturbance of gravel for new nests also contrasted strongly with algae-covered substrate in the surrounding areas, and females rarely abandoned a completed nest prior to dying. It was therefore possible to obtain reliable data on the number of nests they constructed.

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Results

Females studied ranged in length from 40.5 to 76 cm, which is representative of the size range in the stream. They constructed an average of 2.07 ± 0.84 nests with 20 (28.6%), 27 (38.6%), 21 (30.0%), and 2 (2.8%) fish making 1, 2, 3, and 4 nests, respectively. Larger females dug significantly more nests than did smaller ones (comparing female size categories >70, 61–70, 51–60, and <50 cm, $N = 70$, $X = 20.4$, df = 3, $P < 0.01$). Depths of first nests for individual females did not differ significantly from nests they excavated last (paired t-test, $t = 0.695$, $P = 0.5$) (Table 1). Females spawned into each nest they dug. Nests were relatively cone shaped, with the smallest diameter at the bottom where the eggs were laid.

Nest depth averaged 13.7 ± 4.0 cm ($N = 42$); however, nest depth was strongly correlated with female size ($r = 0.778$, $P < 0.01$) (Fig. 1). Large females buried their eggs as much as 2.5-fold deeper than small females. This could result from (1) larger females selecting nest sites that are easier to excavate, (2) larger females having greater strength or a mechanical advantage for lifting gravel, or (3) the greater fecundity of large females necessitating deeper nests. The third alternative is ruled out because the greater egg volume of large females is divided among more nests (see also Hawke 1978). To examine the first two alternatives, we regressed nest depth on both female size and gravel size. The multiple regression (Nie et al. 1975) revealed that 71% of the variance in nest depth is explained by female body size alone ($P < 0.01$) and only 5% is explained by gravel size ($P = 0.57$). Therefore, the second explanation appears to be the most plausible.

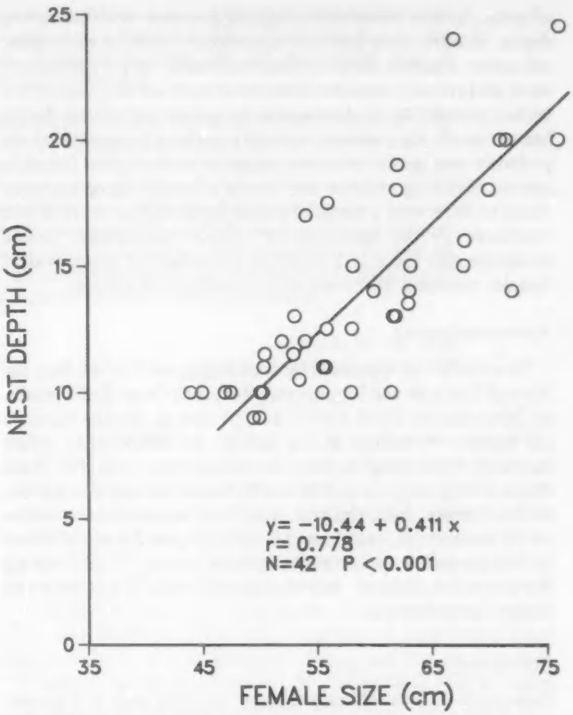

FIG. 1. Nest depth as a function of female size in coho salmon.

TABLE 1. Nest depths of the first and last nests made by 13 female coho salmon. Last row of data is X ± SE.

Female size (cm)	First nest (cm)	Last nest (cm)
46.5	8.9	11.4
50	14.0	15.2
53	11.4	14.0
53.5	12.7	14.0
56	12.7	11.4
56	9.0	11.4
58	10.5	12.5
61.5	14.0	17.8
65.5	22.8	23.4
67	15.2	15.2
68	17.8	16.5
69	20.3	17.8
74	26.7	21.6
59.8 ± 8.3	15.1 ± 5.2	15.5 ± 3.7

Discussion

We have shown that larger females dig deeper nests. Our analysis suggests that the difference in depth is due to a mechanical or energetic advantage from larger body size. Approximately one quarter of the variance in nest depth among females is not explained by body size; however, female energy reserves probably varied considerably. Oceanic ectoparasites were still attached to some of the fish, suggesting that these came directly from the sea. By contrast, some coho were observed in the main river near the mouth of the stream in early September, 2 mo prior to spawning activity. Such disparity in river residence time probably causes considerable variation of energy reserves. Current velocity may account for some variance in nest depth; however, if currents had a major influence, gravel size would have been more strongly correlated with depth, since gravel size is closely linked with current velocity (Novak 1973).

Female salmonids compete aggressively among themselves for nest sites, and eggs are often dug up by later arriving females (Hanson and Smith 1967; McNeil 1962; Schroder 1973; and others). Since larger females bury their eggs as much as 2.5-fold deeper, their broods will be less susceptible to damage from superimposition because there are fewer potential competitors that can dig as deep. Furthermore, due to the cone-shaped nature of nests, the area disturbed by digging decreases with increasing depth. Shallow nests are thus vulnerable to females excavating off center, whereas deep nests are vulnerable only if subsequent nests are precisely centered. Shallower nests are also subject to a higher probability of destruction by gravel movement during heavy runoff. By contrast, mortality costs of deeper burial are probably negligible over the range of nest depths found in nature. Hatching success and alevin mortality have not been found to differ over a range of gravel depth to 30.5 cm (Dill and Northcote 1970). Managers of salmon populations should recognize that there is a selective advantage to larger bodied females resulting from their ability to dig nests deeper.

Acknowledgments

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Uncertainty Analysis of Calculated Nutrient Regeneration Rates in Lake Michigan[1]

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McCormick, M. J., and S. J. Tarapchak. 1984. Uncertainty analysis of calculated nutrient regeneration rates in Lake Michigan. Can. J. Fish. Aquat. Sci. 41: 206–211.

First-order uncertainty analysis of the following error sources was used to estimate errors in a mass balance calculation of regeneration rates for phosphorus, silica, and nitrogen at an offshore station in Lake Michigan: (1) precision of nutrient measurement, (2) vertical eddy diffusivity, (3) atmospheric loading, (4) primary production, (5) nutrient to carbon ratio, and (6) onshore–offshore nutrient transport. Approxi-

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mately 80% of the variance for phosphorus regeneration was due to uncertainty in the phosphorus to carbon ratio, and more than 90% of the variance for silica and nitrogen regeneration was due to the onshore–offshore transport term. Calculated nutrient regeneration rates can be meaningful only if uncertainty due to advection and cellular stoichiometry are minimized.

Dans le but d'évaluer les erreurs dans le calcul du bilan global des taux de régénération du phosphore, du silice et de l'azote à une station au large des rives du lac Michigan, les auteurs ont utilisé une analyse d'incertitude de premier ordre des sources d'erreur suivantes: (1) la précision des mesures des éléments nutritifs, (2) la diffusion toubillonnaire verticale, (3) la charge atmosphérique, (4) la production primaire, (5) le quotient élément nutritif carbone et (6) le transport des éléments nutritifs du rivage vers le large. Environ 80% de la variance de la régénération du phosphore étaient causés par l'incertitude du quotient phosphore carbone. Plus de 90% de la variance de la régénération du silice et de l'azote étaient reliés au facteur du transport côtier–hauturier. Les taux calculés de régénération des éléments nutritifs ne seront significatifs que si l'incertitude attribuable à l'advection et à la stœchiométrie cellulaire est minimisée.

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Factors regulating phytoplankton growth in marine waters have been studied intensively ever since Steemann-Nielsen (1952) introduced the radiocarbon method for estimating primary production. A persistent feature of natural systems where supply rates of nitrogen and phosphorus have been quantified is that phytoplankton growth rates are frequently much higher than theoretically possible based on external nutrient supplies (cf. Barlow and Bishop 1965; Ganf and Blazka 1974; Goldman et al. 1979; Scavia 1979). These results, coupled with laboratory studies of nutrient excretion by herbivorous zooplankton and bacteria mineralization of organic materials, suggest that regeneration in surface waters represents an important nutrient source for phytoplankton. However, with some exceptions (Golterman 1973; Lehman 1980; Stadelmann and Fraser 1974), little work has been done on estimating nutrient regeneration rates and no work has been reported on the errors associated with them.

In general, direct measurement of nutrient regeneration is not yet feasible. Hence, regeneration rates are determined indirectly by mass balance type calculations. These rates mathematically represent the amount of nutrient necessary to identically conserve mass and are calculated by computing the differences between large, imperfectly known terms (e.g. advective versus diffusive nutrient transport). Uncertainty of the true term values is cumulative and, therefore, could be subject to considerable error. In large lakes, these errors may be further enhanced because of greater variability in whole-lake water chemistry than one would expect to find in smaller water bodies. The nonuniform distribution of nutrient sources typical to such regions and the longer time scales required to mix water parcels over larger volumes result in a heterogeneous distribution of material. Hence, the more heterogeneous the water body, the more difficult it is to differentiate between physical and biological control of the recycling process.

Previous estimates of nutrient regeneration rates fail to account for the potential effects of environmental variability and measurement errors on rate estimation. In this report, data on in situ primary productivity, temperature profiles, and nutrient concentrations were analyzed to estimate regeneration rate variances for available phosphorus (P), soluble reactive silica (SiO_2), and available nitrogen (N).

Methods

Sampling and analysis — Sampling was conducted at approximately weekly intervals from May 14 to October 18, 1976, at an offshore station in Lake Michigan (43.09°N, 86.43°W), 90 m in depth, 15 km west of Grand Haven, MI. A string of Niskin bottles equipped with reversible thermometers was used to obtain water at discrete depths between the surface and 25 m. In situ primary production rates were measured by the light and dark bottle ^{14}C method (Strickland and Parsons 1972). Samples in 125-mL reagent bottles were inoculated with $[^{14}C]NaHCO_3$ and usually incubated for 3–5 h between 10:00 a.m. and 4:00 p.m. The entire contents of each bottle were filtered onto 0.45-μm Millipore filters, and excess inorganic ^{14}C was removed by degassing or rinsing with filtered water (Tarapchak et al. 1981). Filters were dried over silica gel, assayed in Aquasol (New England Nuclear, Boston, Mass.) in a Beckman liquid scintillation counter (model LS-150), and corrected for background and quench by the external standards ratio method. Corrections to full-day rates were made by multiplying the incubation measurements by the ratio of total daily solar radiation to solar radiation for the incubation period. Chemical analyses were performed on 0.45-μm Millipore filtered water. Soluble reactive silica (SiO_2) and nitrate nitrogen (NO_3-N) were analyzed by standard methods (American Public Health Association 1976). Soluble reactive phosphorus (SRP) was measured by Harvey's acid molybdate stannous chloride method (Tarapchak and Rubitschun 1981).

Mass balance equations and error estimation — Nutrient concentrations in the epilimnion are described by equation (1):

$$(1)\quad \frac{\partial C_j}{\partial t} + U \cdot \nabla C_j = \nabla \cdot \left(K_H \nabla_H C_j + K_Z \frac{\partial C_j}{\partial Z} \right) + \frac{L_j}{h} + R_j - BQ_j$$

where the coordinate system is right-handed and rotated such that y is shore parallel and positive northward, x is perpendicular to shore and positive eastward, and Z is positive from the surface down, and C_j = concentration of nutrient j, t = time, U = velocity vector (u, v, w) $(m \cdot d^{-1})$, ∇ = gradient operator $(\partial/\partial x, \partial/\partial y, \partial/\partial z)$, ∇_H = horizontal gradient operator $(\partial/\partial x, \partial/\partial y)$, K_H = horizontal eddy diffusivity $(m^2 \cdot d^{-1})$, K_Z = vertical eddy diffusivity $(m^2 \cdot d^{-1})$, L_j = atmospheric loading of nutrient j $(mg \cdot m^2 \cdot d^{-1})$, h = epilimnion depth (m), R_j = regeneration rate of nutrient j $(\mu g \cdot L^{-1} \cdot d^{-1})$, B = primary production rate $(\mu g\, C \cdot L^{-1} \cdot d^{-1})$, Q_j = nutrient j to carbon ratio, and Z = depth (m). Data on nutrient concentrations are insufficient for use in equation (1), but existing data (Bartone and Schelske 1982; Rockwell et al. 1980) suggest that equation (1) may be reduced to a more tractable format by way of the following observations: (1) nutrient isolines tend to parallel lake bathymetry and (2) small horizontal second derivatives exist for all nutrients. Both observations are not necessarily true at any given time because episodic events, such as storms and upwellings, disrupt the longer time average picture. However, for our time scales of interest we assume that these observations approximate the lake environment. Therefore, equation (1) can be simplified by dropping the horizontal eddy diffusion terms and the longshore component of mass flux. An additional simplification is the assumption that vertical advective transport is negligible relative to vertical diffusion. Solving for R_j, equation (1) is reduced to

$$(2)\quad R_j = \frac{\partial C_j}{\partial t} + u\frac{\partial C_j}{\partial X} - \frac{\partial}{\partial Z}\left(K_Z\frac{\partial C_j}{\partial Z}\right) + BQ_j - \frac{L_j}{h}.$$

Terms not explicitly measured during the study were estimated from the literature. Specifically, atmospheric loadings of NO_3, SiO_2, and total P were obtained from Eisenreich et al. (1977) and Eisenreich (1982). The following nutrient to carbon weight ratios were assumed values: $P/C = 0.24$, $SiO_2/C = 1.38$, and $N/C = 0.18$ (Parsons and Takahashi 1973). The B term (equation (2)) was modified for the R_j calculation for SiO_2 by reducing it in proportion to the measured percentage of diatoms contained in the total phytoplankton assemblage. Thermocline diffusivities were calculated from the one-dimensional diffusion equation and data from measured temperature profiles. The magnitude of K_Z was the value that provided the proper heat flux from the epilimnion to balance temporal changes in heat content observed in the hypolimnion. Finally, the onshore–offshore transport term was assumed to be zero; however, its effect on the regeneration rate variance was included as discussed below.

Error estimates of R_j were made by first-order uncertainty analysis, i.e.

$$(3)\quad S^2_{R_j} = \sum_{i=1}^{N}\left(\frac{\partial R_j}{\partial E_i}\right)^2 S^2_{E_i}$$

where E_i = ith error term, $S^2_{E_i}$ = variance of E_i, and $S^2_{R_j}$ = variance of R_j. Six error terms were analyzed and assumed to be uncorrelated so that $S^2_{R_j}$ could be estimated by equation (3). They were (1) precision of nutrient concentration measurement, (2) vertical eddy diffusivity, (3) atmospheric loading, (4) primary production, (5) nutrient to carbon ratio, and (6) onshore–offshore nutrient transport. Variances were calculated either directly from field data or from the literature. An examination of field data statistics suggested a constant coefficient of variation (CV) for C_j, and primary production errors and literature data suggested the same for atmospheric loading and nutrient to carbon ratios. This could not be done for vertical eddy diffusion or onshore–offshore error sources. Variance in K_Z was estimated from the mean square error (MSE), and the MSE was assumed to be equal to the MSE of the paired differences of K_Z calculated from two methods. The first method has already been described, and the second method (Sweers 1970) has been used to provide an estimate of the ability to calculate K_Z precisely. The error calculated by this approach does not explicitly include the natural variability of vertical mixing because of difficulty in making an unambiguous estimate of what is a poorly understood process. Similarly, it should be noted that primary production errors were not based on natural variability but rather on estimates of the errors due to measurement technique. Of the six error terms, the first, second, and fourth are in this category, while the third and fifth are literature based and the last is calculated from current meter data. A summary of the CVs or variances (whichever is time invariant) used in equation (3) is given in Table 1.

The onshore–offshore term, with an assumed zero-mean, was the only error source to have neither a constant CV nor a constant variance. The total transport error considered here is expressed as $(\partial C_j/\partial x)^2 S^2_u$, and the onshore–offshore current variances (S^2_u) were calculated directly from current meter data taken from a nearby station (43.11°N, 86.47°W). Although the current meter mooring and our station are nearly 5 km apart, the currents are probably coherent over this distance (Birchfield and Davidson 1967). The variances were computed for the time intervals corresponding to nutrient measurements. The current meter was located at a depth of 12.5 m, and the data are a subset of those analyzed by Allender and Saylor (1979).

The close proximity of our station to the coastal current suggested that the baroclinic Rossby radius of deformation can be used as the length scale for calculating the onshore gradients. This length scale (5 km was used) is proportional to the width of the coastal current and is a natural choice in such regions. Concentration gradients for offshore and nearshore conditions were estimated for dissolved P, SiO_2, and $NO_3 + NH_3$ from Bartone and Schelske (1982) or were approximated from Rockwell et al. (1980). The gradients were computed by dividing the difference of the offshore and nearshore concentrations by 5 km. The estimated horizontal gradients were 0.00004, 0.02, and $0.0022\ mg \cdot m^{-4}$ for P, SiO_2, and N, respectively.

Results and Discussion

Measured surface water temperatures range from 6°C in mid-May to 21°C in mid-August, and data indicate at least one upwelling event during this period. Primary production normally occurred to depths of 25–30 m, with mean epilimnetic rates ranging from lows of 8.3 (May 14) and 12.9 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$ (October 18) up to 59.2 $\mu g\ C \cdot L^{-1} \cdot d^{-1}$ (July 7) (Fig. 1d). Epilimnetic SiO_2 concentrations were generally higher in May and October ($>1\ mg\ SiO_2 \cdot L^{-1}$) than during summer and often were variable with depth (Fig. 1b). Similarly, mean epilimnetic NO_3-N concentrations were highest during May (>0.23 mg $NO_3\text{-}N \cdot L^{-1}$) and were reduced to levels $<0.15\ mg\ NO_3\text{-}N \cdot L^{-1}$ during mid- to late August and then progressively increased through September and October (Fig. 1c). SRP concentrations, ranging from 2.1 (September 7) to 8.2 $\mu g\ P \cdot L^{-1}$ (July 14), were highly variable and showed, on an average, weaker vertical gradients than the other nutrients (Fig. 1a).

We used SRP as an estimator of biologically available P, which is consistent with experimental results (Cowen and Lee 1976; Chamberlain and Shapiro 1969) and previous attempts (e.g. Stadelmann and Fraser 1974) to calculate P regeneration. Our values on average are higher than those of Bartone and Schelske (1982), who used the ascorbic acid method. These apparent discrepancies have been traced to method-specific differences caused by variations in acid strength and molybdate concentration (Tarapchak et al. 1982). Even if biologically available P is overestimated by Harvey's method (Tarapchak and Rubitschun 1981) or underestimated by the ascorbic acid method, our regeneration rate estimates are not invalidated because rates of change in concentration rather than absolute values of SRP are used in the calculation. Therefore, it is not necessary to estimate each term in equations (2) and (3) by the same procedure but rather to ensure that all methods used in the

TABLE 1. Time invariant components of the error terms.

Error term	Variance	Coefficient of variation (SD/mean × 100)	Source
1. Measurement precision			
2. Vertical eddy diffusivity ($m^4 \cdot d^{-1}$)	260	5	This study
3. Atmospheric loading			
P^a		32	Eisenreich et al. 1977
SiO_2		56	Eisenreich et al. 1977
$NO_3{}^b$		56	This study
4. Primary production		10	This study
5. Nutrient to carbon ratio			
P/C	0.00054	97	Canale et al. 1974
SiO_2/C	2.12	114	Canale et al. 1974
N/C	0.0036	33	Canale et al. 1974

[a] Loading rate expressed as total P, where 60% is assumed to be mobilizable by biota.
[b] Loading rate from Eisenreich (1982) and CV is assumed to be equal to that for SiO_2.

analyses show similar responses to changes in P pool concentrations.

Equation (2) was solved numerically for a two-layered fluid. Measurements were averaged over appropriate depths (Fig. 1), and time derivatives were approximated forward in time. Calculations of both R_j and $S^2_{R_j}$ were made for all except two dates. On July 7 and 29, calculated values of K_Z were negative, indicating failure of the one-dimensional assumption that local temperature profiles are controlled by local processes. Hence, no rates were determined.

Phosphorus regeneration rates are all positive (Fig. 2a); however, SiO_2 and N (Fig. 2b and 2c) are negative on several dates. When averaged over the entire study period, the mean regeneration rates ($\mu g \cdot L^{-1} \cdot d^{-1} \pm 1$ SD) for P, SiO_2, and N are 0.82 ± 0.24, -11.3 ± 47.0, and 2.3 ± 5.1, respectively. The P estimates are the most precise, and the SiO_2 estimates the least precise.

Negative rates may result when a nutrient sink or an advective source is neglected, or when their true values are underestimated. For example, if on any date the net phytoplankton growth rate is underestimated, then so are the calculated regeneration rates. The occurrence of negative values, whether they occur on one day or represent a seasonal average, demands an examination of error sources.

Two different estimates of standard deviation for regeneration rates of P, SiO_2, and N were computed. The larger estimate resulted from summing all terms (equation 3)), while the smaller standard deviation is the same estimate minus the onshore–offshore term (Fig. 2). The size of the regeneration rate error bars graphically demonstrates that the calculated rates are not significant. Statistical significance could not be attained by setting the u velocity component in equation (2) from zero to the calculated mean values from the nearby current meter mooring. In all but one case, the individual rate values were not significantly different from zero. However, error analysis identified two major sources of uncertainty large enough that their minimization alone would allow statistically significant nonzero rate estimates. One major source of uncertainty in estimating SiO_2 and N regeneration rates was horizontal mass transport, accounting for 93 and 95% of the variance, respectively. The second major error source was the P/C ratio, which contributed more than 80% to the P regeneration error. Horizontal mass transport could explain, on the average, only 16% of the variance.

Of the remaining error terms, atmospheric loading was negligible for all nutrients. Lack of precision in measuring nutrient concentration and primary production rates was also unimportant, representing less than 1% of the total error. Vertical eddy diffusivity contributed approximately 3% to the SiO_2 and N errors and was comparable with that found for the nutrient to carbon ratios.

Dominance of P/C over advection error is surprising when compared with results for SiO_2 and N. Nutrient to carbon error as a percentage of total error for SiO_2 and N was unimportant for both nutrients even though the CV for SiO_2/C was greater than that for P/C (Table 1). The importance of P/C uncertainty suggests that advection is unimportant to P cycling because of the smaller horizontal gradients in P. Estimated P gradients are 55 times smaller than N and 500 times smaller than SiO_2. The gross dissimilarities in nutrient gradients, in addition to the error analysis, can be interpreted to mean that biological processes dominate over physical processes in P regeneration. Low concentrations of available P, and low horizontal P gradients, are maintained by P-limited phytoplankton, which rapidly take up and store exploitable nutrient concentrations when they encounter them. Under these conditions the phytoplankton control regeneration error by effecting a more homogeneous distribution of available P, and thus reducing the advective influence that would otherwise occur.

Although P is the only nutrient here to behave in this manner, it does not preclude the possibility of mimic by other nutrients. Similar results can be expected for any nutrient in lake or marine waters that limits algal production, provided that limiting conditions persist long enough to resolve their effects. For example, if advection errors for SiO_2 regeneration were to diminish because of limitation effects, then SiO_2 would have to limit diatom growth for both sufficient time and area to show a reduction in difference between mean offshore and onshore nutrient concentrations. This was not obvious in our study and is probably a consequence of how the horizontal gradients were estimated.

Values for the horizontal nutrient gradients represented mean

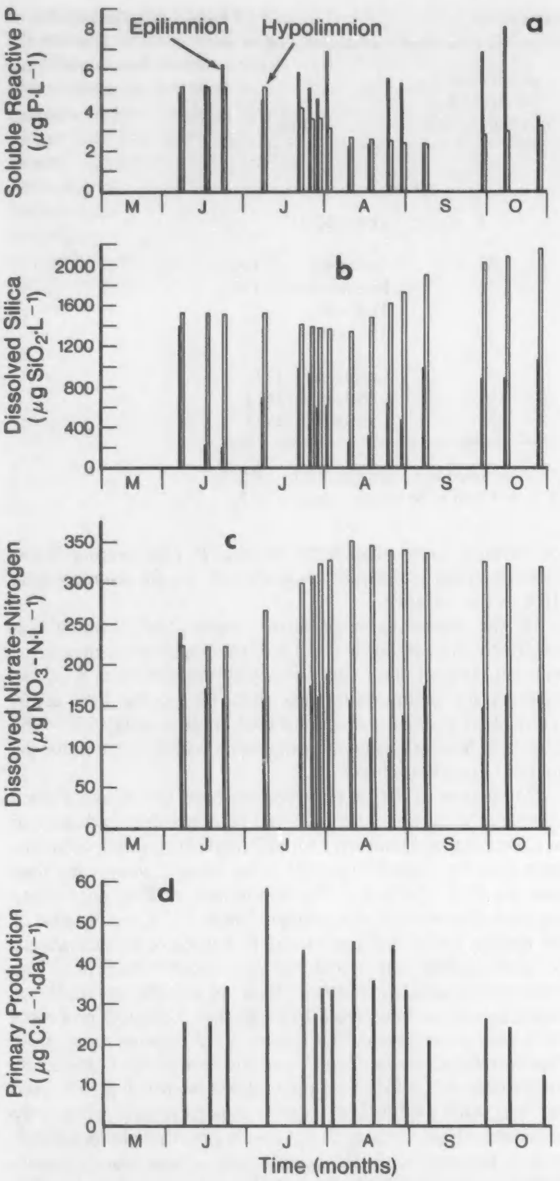

FIG. 1. Epilimnetic and hypolimnetic averaged nutrient measurements and epilimnetic averaged primary production rate for an offshore station in Lake Michigan in 1976. (a) Soluble reactive P; (b) dissolved reactive SiO_2; (c) dissolved NO_3-N; (d) primary production rate.

seasonal conditions. If data were available to estimate gradients on shorter time scales, then it would perhaps be possible to detect error patterns emerging where advection alternates with nutrient to carbon ratio as the major source of uncertainty. The probable error patterns would more closely follow environmental dynamics and would enable data to be sequenced into more homogeneous groupings, with different means and lower variances than seasonal values. However, without the benefit of such information, seasonal values must be substituted.

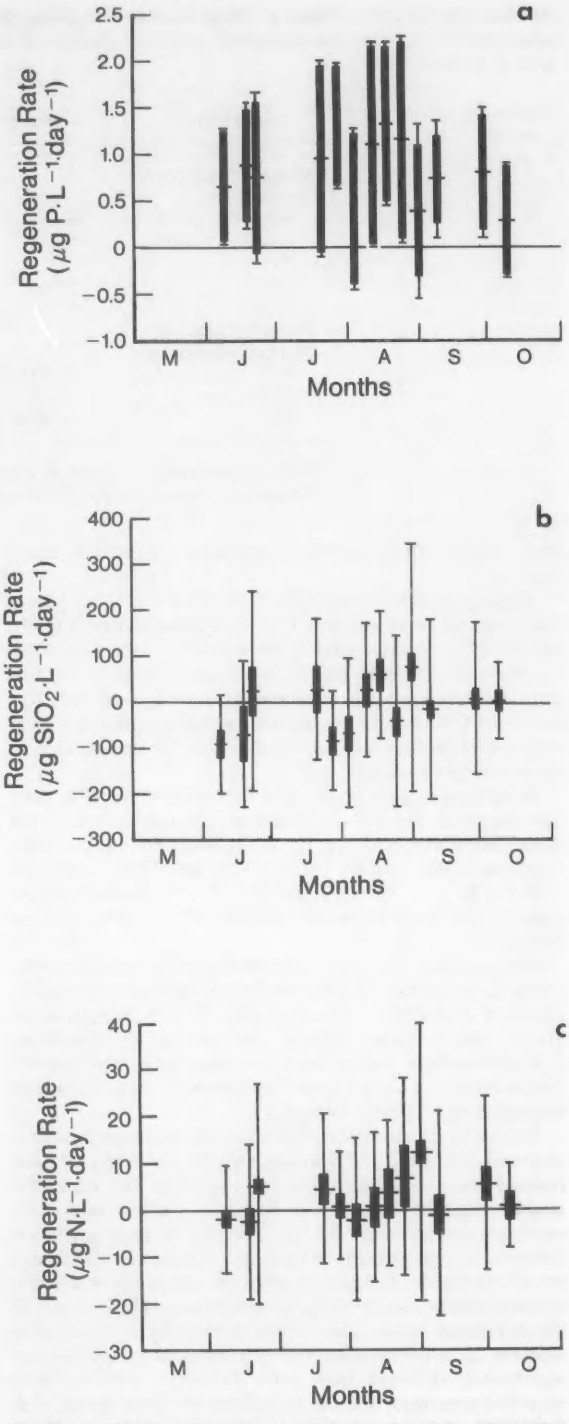

FIG. 2. Available regeneration rates ± 1 SD for (a) P, (b) reactive SiO_2, and (c) available N. The smaller, blackened SD bar represents all error terms minus the error due to onshore–offshore transport. The larger SD bar represents all error terms.

Although rate estimates may be rejected because of overestimated errors, the approach does provide a reasonable basis for identifying and assessing seasonally dominant regeneration errors.

Concluding Remarks

High variability in nutrient to carbon ratios can become a major source of error for limiting nutrients, such as P. In these situations, advective errors are diminished but not eliminated because, in effect, they are manifested in increased intracellular nutrient variability in the phytoplankton population. Our work clearly shows that substantial errors from these processes arise in estimation of nutrient regeneration rates and that they are large enough to mask meaningful insights into the recycling process. This scenario is likely to occur in any water body. The extent to which it is a concern for large lakes, such as the Great Lakes, is unmistakable, but the importance of these error sources for smaller lakes must be redetermined.

If future determinations of nutrient regeneration rates based on mass balance calculations are to be credible, then the uncertainty due to horizontal mass transport, or in the case of P, cellular stoichiometry, must be minimized. Attempts to meet both criteria may not always be feasible, but we recommend that future calculations of P regeneration at least quantify the temporal variability of intracellular P and/or any other limiting nutrient.

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Comparison of Three Methods for Estimating the Food Intake of a Fish

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Majkowski, J., and W. S. Hearn. 1984. Comparison of three methods for estimating the food intake of a fish. Can. J. Fish. Aquat. Sci. 41: 212–215.

Majkowski and Waiwood's (1981. Can. J. Fish. Aquat. Sci. 38: 1199–1206) method for evaluating the food intake of a fish involves numerically solving a first-order ordinary differential equation and using a minimization procedure. In this note, that method is compared with its two modifications created by (1) the elimination of a mathematical approximation ("improved method") (but this makes the food intake estimation computationally even more difficult), and (2) the introduction of a different mathematical approximation ("simplified method") to involve only simple algebraic calculations. As a result of the latter modification, a certain assumption in the original and improved methods is relaxed and the required experimental information is reduced. Growth and bioenergetic data concerning Gulf of St. Lawrence cod (*Gadus morhua*) are used to illustrate the three methods and to examine the validity of the mathematical approximations introduced. The use of the original method results in larger errors in food intake estimates for cod than the simplified method. The food intake estimates using the improved method differ considerably (by 3.6–23.5% and 1.7–10.4%, respectively) from those based on the original and simplified methods, if the corresponding ratio of the weight increment to the initial weight is large (>2.3).

Dans la méthode de Majkowski et Waiwood (1981. J. can. sci. hal. aquat. 38: 1199–1206) d'évaluation de la quantité de nourriture consommée par un poisson, il s'agit de résoudre numériquement une équation différentielle ordinaire du premier ordre et d'utiliser une procédure de minimisation. Dans le présent commentaire, cette méthode est améliorée (1) en éliminant une approximation mathématique (mais cela rend le calcul estimatif de la consommation de nourriture encore plus difficile) et (2) en introduisant une approximation mathématique différente n'exigeant que de simples calculs algébriques. Par suite de la dernière simplification, une certaine hypothèse dans les méthodes originale et améliorée est supprimée et l'information expérimentale requise est réduite. Les données sur la croissance et la bioénergie relatives à la morue du golfe St-Laurent (*Gadus morhua*) sont utilisées pour illustrer les trois méthodes et pour évaluer la validité des approximations mathématiques introduites. L'emploi de la méthode originale entraîne de plus grandes erreurs dans les estimations de la consommation de nourriture pour la morue que la méthode simplifiée. Les estimations de la consommation de nourriture faites à partir de la méthode améliorée diffèrent considérablement (de 3,6 à 23,5% et de 1,7 à 10,4% respectivement) de celles faites à partir des méthodes originale et simplifiée, si le rapport correspondant entre l'accroissement de poids et le poids initial est grand (>2,3).

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The importance of and difficulties involved in obtaining information on the amount of food consumed by a fish population have been emphasized by many investigators. The feeding rate of fish in nature is usually evaluated by (i) using estimates of gut contents and gastric evacuation rates, (ii) simulating natural conditions in the laboratory and measuring the food intake or directly extrapolating these measurements, or (iii) using mathematical models relating fish growth to food consumption (see reviews in Conover 1978; Mann 1978; Majkowski and Waiwood 1981).

The estimation of fish food intake, ΔR, during a period Δt using method iii is made on the basis of the following equation or its modifications:

$$(1)\quad \Delta R = (\Delta w + \Delta E + \Delta T)/\beta$$

where Δw is the increment of body weight during Δt, ΔE denotes losses of reproductive products during Δt, ΔT is the sum of all metabolic losses during Δt, and β is the relative fraction of food intake assimilated but not excreted (for examples, see references below). Reproduction and excretion losses are frequently treated as negligible when ΔR is calculated. Parameters Δw and ΔE can usually be estimated on the basis of field sampling (Kerr 1982). Because parameter β is regarded by most investigators as relatively independent of feeding rate, food composition, fish body size, and temperature (see reviews in Winberg 1956; Gerkins 1978; Mann 1978), its value determined in laboratory conditions is usually used. The real difficulty in the use of equation (1) occurs in the estimation of ΔT (Adams et al. 1982). This parameter can usually be determined in the laboratory only and is strongly dependent on weight, temperature, and feeding rate (see reviews in Kerr 1971, 1982; Ursin 1979; Majkowski and Waiwood 1981). The dependence of ΔT on the first two parameters is relatively well identified and values of these parameters can usually be monitored. The proper account of the dependence of ΔT on the third parameter is most difficult.

Most investigators (i) assume, using the Winberg (1956) rule, that the value of ΔT is not affected by the magnitude of ΔR (e.g.

Mann 1965; Backiel 1971; Fagerström and Asell 1973), (ii) assume that only one of the ΔT components, Specific Dynamic Action (SDA), is dependent on ΔR (e.g. Norstrom et al. 1976; Kitchell et al. 1977; Kitchell and Breck 1980; Minton and McLean 1982; Stewart et al. 1983) or on Δw (e.g. Sharp and Francis 1975), or (iii) estimate the range of possible ΔT values and, consequently, obtain a wide range of ΔR values (e.g. Stillwell and Kohler 1982). Because both SDA and the rate of catabolism related to physical activities are dependent on ΔR (see references above), methods (i) and (ii) may introduce a considerable bias to food intake estimates (Majkowski and Waiwood 1981).

Attempts to more properly account for the dependence of ΔT on ΔR are made by Majkowski and Waiwood (1980, 1981), Waiwood et al. (1980), Waiwood (1981), Kerr (1982), Waiwood and Losier (1982), and Waiwood and Majkowski (1984). The relationship applied by Kerr (1982) is slightly different from that used by the remaining researchers. Additional properly designed empirical studies are necessary to evaluate which of the two relationships is more correct. Kerr (1982) considered 1 yr as the smallest time increment, Δt, in his procedure and, consequently, used difference equations. The remaining researchers considered infinitely small time increments and used differential equations. The use of differential equations is theoretically more correct in this case, especially if accurate data and a growth model are available, but it makes the estimation of ΔR computationally more difficult.

In this note, the method developed by Majkowski and Waiwood (1980, 1981), and subsequently used by Waiwood et al. (1980), Waiwood (1981), and Waiwood and Losier (1982), is improved by the elimination of a mathematical approximation. This improvement makes the food intake estimation computationally even more difficult. It is also demonstrated that the Majkowski and Waiwood (1980, 1981) method may be simplified by the introduction of a different mathematical approximation to involve only simple algebraic calculations. As a result of this simplification, certain assumptions associated with the original and improved methods are relaxed and the required experimental information is reduced. Growth and bioenergetic data concerning cod (*Gadus morhua*) are used to illustrate the three methods and to examine the validity of the mathematical approximations.

Original method (O)

Majkowski and Waiwood's (1981) method is based on Ursin's (1979) modified equation:

$$(2)\quad \frac{dw_i}{dt} = (1-\alpha_i)\beta_i \hat{H}_i' w_i^{m_i} - k_i w_i^{n_i}$$

where subscript i identifies constants and variables with respect to age classes and years, w_i is body weight (excluding reproductive products), t denotes time (years), α_i is the relative fraction of assimilated food lost in feeding catabolism (i.e. total catabolism reduced by fasting catabolism; feeding catabolism includes SDA and catabolism related to physical activities above the fasting level), β_i is the relative fraction of food assimilated but not excreted, $\hat{H}_i' w_i^{m_i}$ can be interpreted as the instantaneous intake rate of food utilized for somatic growth and body (excluding reproductive products) maintenance only ($\hat{H}_i'$ is dependent on food availability, temperature, etc.), and $k_i w_i^{n_i}$ is the instantaneous rate of fasting catabolism. To apply this method, the values of m_i, n_i, and k_i (k_i varies due to temperature changes) have to be known for any given moment during the period Δt_i. Parameters α_i and β_i have to be determined as known functions of $\hat{H}_i' w_i^{m_i}$, temperature, time, etc. The method can be applied even if $\hat{H}'$ is a function of time or temperature whose form (but not necessarily parameter values) is known; it is assumed in this note that $\hat{H}_i'$ is a parameter. Empirical methods for estimating α_i, β_i, m_i, k_i, and n_i are listed in Majkowski and Waiwood (1981). Parameter $\hat{H}_i'$ can be estimated by adjusting it to obtain agreement between growth data and the solution of differential equation (2). The food intake, ΔR_{Oi}, during the period Δt_i (defined as $t_{i+1} - t_i$) is then calculated on the basis of the following equation:

$$(3)\quad \Delta R_{Oi} = \Delta t_i \hat{H}_i' \bar{w}_i^{m_i} + \frac{\Delta E_i}{(1-\alpha_i)\beta_i}$$

where $\bar{w}_i$ is equal to $0.5[w_i(t_i) + w_i(t_{i+1})]$ or $w_i[0.5(t_i + t_{i+1})]$ depending on data availability and ΔE_i is the biomass of reproductive products produced during the period (t_i, t_{i+1}).

Improved method (I)

The term $\hat{H}_i' \bar{w}_i^{m_i}$ in equation (3) is a mathematical approximation of the integral of $\hat{H}_i'[w_i(t)]^{m_i}$ over the period (t_i, t_{i+1}). Hence, if equation (2) closely reflects fish growth, the food intake can be estimated more accurately using the following equation:

$$(4)\quad \Delta R_{Ii} = \hat{H}_i' \int_{t_i}^{t_{i+1}} [w_i(t)]^{m_i} dt + \frac{\Delta E_i}{(1-\alpha_i)\beta_i}$$

instead of equation (3), where $w_i(t)$ is the solution of differential equation (2). The computation of ΔR_{Ii} is more complex than that of ΔR_{Oi}, because it involves numerically integrating $\hat{H}_i'[w_i(t)]^{m_i}$ in addition to the estimation of $\hat{H}_i'$.

Simplified method (S)

The first term on the right-hand side of equation (4) is the intake ($\Delta R_i'$) of food utilized for somatic growth and body maintenance during the period (t_i, t_{i+1}). To calculate this term in an alternative way, the term $\hat{H}_i' w_i^{m_i}$ in equation (2) has to be replaced by its more general equivalent, dR_i'/dt (the instantaneous intake rate of food utilized for somatic growth and body maintenance). Integrating both sides of such an equation and rearranging certain terms, the following equation can be obtained:

$$(5)\quad \Delta R_i' = \frac{\Delta w_i + \int_{t_i}^{t_{i+1}} k_i w_i^{n_i} dt}{(1-\alpha_i)\beta_i}$$

where Δw_i is equal to $w_i(t_{i+1}) - w_i(t_i)$. The integral in equation (5) may be approximated by $\Delta t_i k_i \bar{w}_i^{n_i}$. Hence, equation (4) may be simplified to the following form:

$$(6)\quad \Delta R_{Si} = \frac{\Delta w_i + \Delta t_i k_i \bar{w}_i^{n_i} + \Delta E_i}{(1-\alpha_i)\beta_i}.$$

Example

The 1956 cohort of cod (*Gadus morhua*) population inhabiting the southern Gulf of St. Lawrence (NAFO subarea 4T) and the edge of the Laurentian Channel off the northeast coast of Cape Breton (NAFO subarea 4Vn) was chosen to test the methods. This population spawns approximately in midyear. Fish becoming i yr old in the year under consideration are referred to as age-class i (see Table 1).

TABLE 1. July 1 and January 1 weights (w_{Ji}) for age-class 0 and age-classes 1–21, respectively, for the 1956 cod cohort (Lett 1978), half-yearly and yearly food intakes (ΔR_{Ii}) calculated on the basis of equation (4), relative differences between ΔR_{Ii} and the corresponding food intakes ΔR_{Oi} estimated using equation (3), and relative differences between ΔR_{Ii} and the corresponding food intakes ΔR_{Si} evaluated on the basis of equation (6).

Age-class[a]	Year	w_{Ji} (g)	ΔR_{Ii} (g)	$\frac{\Delta R_{Oi} - \Delta R_{Ii}}{\Delta R_{Ii}}$ (%)	$\frac{\Delta R_{Si} - \Delta R_{Ii}}{\Delta R_{Ii}}$ (%)
0	1956	1[b]	30.9	14.59	4.43
1	1957	12[c]	172.5	6.12	2.91
2	1958	60	507.8	3.61	1.74
3	1959	200	1658.5	4.15	1.76
4	1960	700	1361.4	−0.02	−0.04
5	1961	840	1662.6	−0.01	−0.03
6	1962	1020	1748.0	−0.03	−0.05
7	1963	1150	1716.9	−0.02	−0.03
8	1964	1210	2619.5	0.07	0.02
9	1965	1580	3032.2	0.01	−0.01
10	1966	1940	3694.3	0.02	−0.00
11	1967	2390	7965.6	0.76	0.39
12	1968	4260	10401.5	0.27	0.15
13	1969	6230	7611.1	−0.00	−0.01
14	1970	6290	9120.0	−0.01	−0.02
15	1971	6890	9712.8	−0.01	−0.02
16	1972	7451[d]	10262.0	−0.01	−0.02
17	1973	7973[d]	10772.7	−0.01	−0.02
18	1974	8458[d]	11239.0	−0.01	−0.02
19	1975	8905[d]	11667.4	−0.01	−0.02
20	1976	9316[d]	12065.4	−0.01	−0.01
21	1977	9695[d]	12426.7	−0.01	−0.01

[a] Age-class *i* consists of fish becoming *i* yr old in the calendar year indicated in the second column.

[b] This value is assumed to be the July 1 weight.

[c] This value is calculated on the basis of equation (2), the initial weight of 1 g (i.e. w_{J0}), the values of α_i, β_i, m_i, k_i, and n_i from the Example section, and $\hat{H}_i'$ adjusted to obtain agreement between the solution of differential equation (2) and w_{J0} and w_{J2}.

[d] This value is calculated on the basis of equation (2), the initial weight of 6890 g (i.e. w_{J15}), the values of α_i, β_i, m_i, k_i, and n_i from the Example section, and $\hat{H}_{14}'$ adjusted to obtain agreement between the solution of differential equation (2) and w_{J14} and w_{J15}.

To examine the validity of the mathematical approximations introduced in methods O and S, ΔR_{Ii} values ($i = 0, \ldots, 21$) are calculated initially and these values are then compared with corresponding ΔR_{Oi} and ΔR_{Si} values. The period (t_i, t_{i+1}) for $i = 0$ is selected as July 1–December 31, 1956. The periods (t_i, t_{i+1}) for $i = 1$ to 21 are chosen as January 1–December 31, 1956, + *i*.

The same values of α_i (0.4), β_i (0.8), m_i (0.56), and n_i (0.83) are used as those applied by Majkowski and Waiwood (1981). The values of ΔE_i are estimated using the same method (and values of *a* ($0.0052g^{1-b}$), *b* (1.38), and p_i (0% for age-classes 0, 1, and 2, 31 and 81% for age-classes 3 and 4, respectively, and 100% for age-classes 5–20)) as that used by Majkowski and Waiwood (1981). The midyear weights $\bar{w}_i$, required for the estimation of ΔE_i ($= p_i a \bar{w}_i^b / 100\%$) are assumed to be equal to the mean values calculated on the basis of the growth date from Table 1 ($\bar{w}_i = (w_{Ji} + w_{Ji+1})/2$).

On the basis of Kohler's (1964) data, Majkowski and Waiwood (1981) estimated k_i for cod inhabiting the southern Gulf of St. Lawrence and the edge of the Laurentian Channel off the northeast coast of Cape Breton as equal to $2.94\ g^{1-n_i} \cdot yr^{-1}$. Because they identified that food intake estimates are sensitive to changes in this estimate, efforts are made to improve the estimate. The mean temperature associated with the Kohler (1964) experiment was estimated to be 8.3°C whereas the mean bottom temperatures in the abovementioned area fluctuate annually from 0.61 to 4.43°C (Waiwood and Majkowski 1984). Hence, the initial estimate of k_i was adjusted using the Jones and Hislop (1979) method to account for the difference between the mean temperature related to the Kohler (1964) experiment and that of 2.9°C (average temperature) for the areas of interest. The k_i value of $1.9\ g^{1-n_i} \cdot yr^{-1}$, which is derived in this way is in a good agreement with that of $2.0\ g^{1-n_i} \cdot yr^{-1}$, which is used by Ursin (1979) for North Atlantic cod.

The half-yearly increment of weight for age-class 0 and the yearly increments of weight for age-classes 1–20 (Δw_i) are calculated on the basis of average July 1 and January 1 weights (w_{Ji}) from Table 1.

The food intakes (ΔR_{Ii}) calculated on the basis of equation (4) are presented in Table 1. The ΔR_{Oi} values calculated using equation (3) differ by −0.03 to 14.59% from the corresponding ΔR_{Ii} values (see Table 1). The large differences (greater than 0.8%) exist only for age-classes 0–3. The differences between ΔR_{Ii} and ΔR_{Si} values are generally smaller (−0.05 to 4.43%) than the corresponding differences between ΔR_{Ii} and ΔR_{Oi} values.

If Δt_i intervals smaller than those described above are applied, the results obtained from the three methods are less distinguishable than those in Table 1. For example, if the July 1 weight for age-class 1 is generated similarly as described in footnote c to Table 1 and half-a-year Δt intervals are applied for this age-class, the yearly food intakes calculated on the basis of the original and simplified methods differ by 1.7 and 0.8%, respectively, from that evaluated using the improved method.

However, if Δt_i intervals greater than ½ yr for age-class 0 and 1 yr for the remaining age-classes are applied, the differences between food intake estimates derived on the basis of the three methods become larger than those in Table 1. For example, increasing Δt_i by only ½ yr (January 1–December 31, 1957, to July 1, 1956–December 31, 1957) results in 23.5 and 10.4% errors in the food intake estimates if the original and simplified methods, respectively, are used. If Δt of 17 yr associated with the initial and terminal weights of 700 and 9695 g, respectively (see Table 1), is applied, the 17-yr food intakes calculated on the basis of the original and simplified methods differ by −2.4 and −5.6%, respectively, from that evaluated using the improved method.

Discussion

The example presented indicates that the use of the approximation in the original method results in larger errors in food intake estimates, at least for cod, than the application of the different approximation in the simplified method. Therefore, there is no advantage to use the original method for cod, which is computationally nearly as complex as the improved method. Also, the original method, like the improved method, but unlike the simplified method, necessitates the instantaneous intake rate of food utilized for somatic growth and body maintenance to be a power function of fish body weight. As a consequence, the value of m_i is eliminated in the simplified method from the set of input data required. These are the two further advantages of the simplified method. However, the presented examples of large differences between ΔR_{Ii} and ΔR_{Si} values highlight the necessity of using the improved method rather than the simplified method in certain cases.

The food intake estimates derived using the improved method differ considerably (i.e. 3.6–23.5% and 1.7–10.4%) from those based on the simplified and original methods, respectively, if the corresponding ratio of the weight increment to the initial weight is large (>2.3). For example, the Δt intervals of $\frac{1}{2}$ and 1 yr for age-classes 0 and 1–3, respectively, are too large to make the food intake estimates obtained on the basis of the three methods similar for these age-classes, whereas the Δt intervals of 1 yr for age-classes 4–20 are sufficiently small to result in very similar estimates of ΔR_{Ii}, ΔR_{Oi}, and ΔR_{Si}. This is because cod belonging to age-classes 0–3 grow much faster relative to initial weight than those belonging to age-classes 4–20. The effects of decreasing and increasing the abovementioned Δt intervals can be interpreted in a similar way.

It is emphasized that the quantitative conclusions reached in this note may not be valid for fish other than cod inhabiting the southern Gulf of St. Lawrence and the edge of the Laurentian Channel off the northeast coast of Cape Breton or even for time increments other than those examined. These conclusions directly concern the three food intake estimation methods based on Ursin's (1979) equation, but they also allow us to make a more general observation. Food intake estimates are usually calculated using finite-difference equations and large time increments rather than infinitely small increments and differential equations and integrations. As demonstrated in this note, such an estimation may be in error, especially for fast-growing fish, due to mathematical oversimplification.

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PERSPECTIVES

The Seventy-Fifth Anniversary of Two Canadian Biological Stations

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Needler, A. W. H. 1984. The seventy-fifth anniversary of two Canadian biological stations. Can. J. Fish. Aquat. Sci. 41: 216–224.

The evolution of the Biological Stations established by the Government of Canada at St. Andrews, N.B., and Nanaimo, B.C., in the summer of 1908 is outlined from small operations with limited facilities ashore and afloat manned seasonally by volunteer university scientists to modern well-equipped laboratories used by year-round scientific and technical staffs. The excellence of the work of the two stations depended on the independence and scientific integrity of the Biological Board (1912–37) and the Fisheries Research Board (1937–73) with memberships combining representatives of government and industry with a majority of university scientists. Under the Board the stations maintained a high level of efficiency and a good balance between short- and long-term and between fundamental and applied research. Programs were responsive to the needs of government and industry and made important contributions to fisheries management and development both domestic and international in both the Atlantic and the Pacific. It is hoped that the new regime may be modified to enable the stations to continue the level of excellence achieved under the Board.

Nous esquissons dans l'article qui suit l'évolution des stations biologiques que le gouvernement du Canada fondait à St. Andrews (N.-B.) et à Nanaïmo (C.-B.) à l'été 1908, depuis des opérations de faible envergure, avec installations limitées à terre et en mer, occupées saisonnièrement par des scientifiques universitaires bénévoles, d'une part, à des laboratoires modernes, bien équipés, utilisés à l'année longue par un personnel scientifique et technique, d'autre part. L'excellence des travaux des deux stations est due à l'indépendance et à l'intégrité scientifique du conseil biologique (1912–1937) et de l'office des recherches sur les pêcheries (1937–1973), formé de représentants du gouvernement et de l'industrie, et de scientifiques des universités, ces derniers étant majoritaires. Sous l'égide de l'office, les stations maintinrent un haut niveau d'efficacité et un sain équilibre entre recherche à court et à long terme, et entre recherche fondamentale et appliquée. Les programmes, répondant aux besoins du gouvernement et de l'industrie, contribuèrent énormément à la gestion des pêches et au développement des sciences halieutiques, à échelle tant nationale qu'internationale, dans l'Atlantique comme dans le Pacifique. Il est à souhaiter que le nouveau régime pourra être modifié pour permettre aux stations de maintenir le niveau d'excellence atteint sous le régime de l'office.

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In the summer of 1908 Canada established biological stations at both St. Andrews, New Brunswick, and Nanaimo, British Columbia. The frame buildings built at that time have long been replaced, but the sites have been used continuously as headquarters for research that has firmly placed these stations in the forefront of the world's attack on scientific problems related to fisheries, and has well justified the faith and foresight of the founders.

The seventy-five years have witnessed growth from the early beginnings of Canadian marine biology, when valuable exploratory research was carried out mainly in the summers by volunteer university scientists with limited facilities ashore and afloat, to the modern well-equipped laboratories and research vessels now used by year-round scientific and technical staffs. They have witnessed the development and decline of a unique and highly successful institution in the Fisheries Research Board, which gave Canada excellent service and an honorable international reputation. They have witnessed the transition from academic studies, regarded with scepticism by many in industry and government, to research well directed to the solution of important fisheries problems and regarded by all concerned as an essential step in best use of the fisheries resource.

Having been closely associated with both stations for many years, I was honored and pleased when asked to write a short article on the occasion of their seventy-fifth anniversary. Directors and scientists of both stations were consulted, but the views expressed are my own. I must also accept responsibility for selection of the highlights to be mentioned. In a short article many worthy and important matters are inevitably omitted. For greater detail the reader is referred to *The Aquatic Explorers: A History of the Fisheries Research Board of Canada* Johnstone

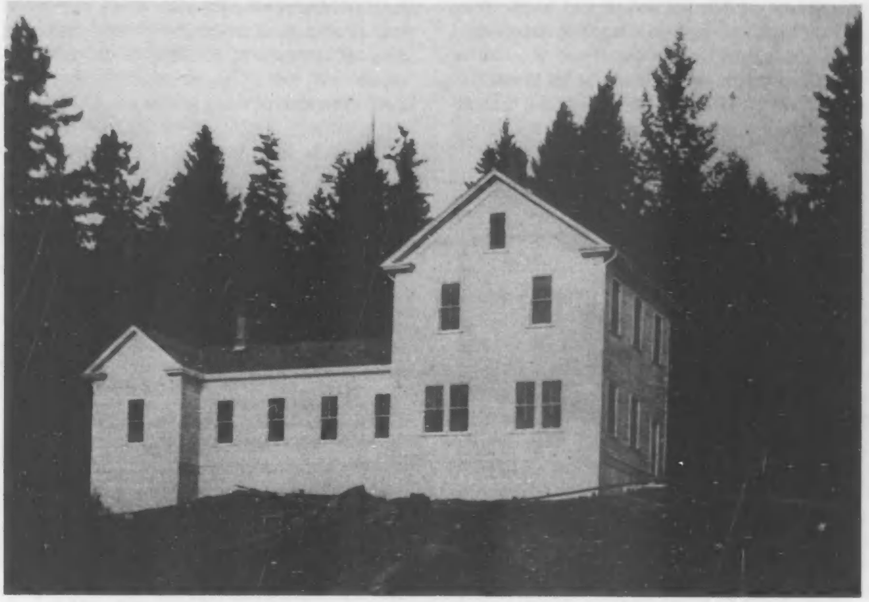

FIG. 1. The Pacific Biological Station, Nanaimo, B.C., soon after completion in 1908. It contained working space for eight scientists, office, library, photographic darkroom, and four bedrooms for visiting scientists. An adjoining building housed kitchen and caretaker's quarters.

(1977) and to articles by the two Directors on the occasion of the fiftieth anniversaries of the Biological Stations (Hart 1958; Needler 1958). Ricker (1975) summarized the Board's achievements in research to that time. In view of the details already published in these articles, I have avoided details here. If I started mentioning names of research scientists I would not know where to stop.

Early Beginnings

In the latter half of the nineteenth century there was a great awakening of interest in the plants and animals of the oceans and the conditions under which they live. The world-girdling voyage of H.M.S. *Challenger* was the greatest of several deep-ocean research cruises. The establishment of the first marine biological laboratory at Naples in 1872 was soon followed by many others in Europe and North America. The importance of research to fisheries was so widely recognized before the end of the century that in 1899 the International Council for the Exploration of the Sea was founded to coordinate European research and became the first international fisheries body.

In Canada a number of far-sighted scientists, seeing developments in the United States such as the Woods Hole and Friday Harbor laboratories, proposed the establishment of biological stations for fisheries, and they were supported by resolutions of the Royal Society of Canada in 1896 and of the British Association for the Advancement of Science when it met in Toronto in 1897. In 1893 the government, apparently aware of the potential value of fisheries science, had already appointed, as Commissioner of Fisheries, Dr E. E. Prince who brought with him Scottish experience in the field.

In 1898, Parliament appropriated $5000 for the construction of a movable laboratory and $2000 for its operation for 1 yr! This laboratory was at St. Andrews, N.B., in 1899 and 1900, at Canso, N.S., in 1901 and 1902, at Malpeque, P.E.I., in 1903 and 1904, and at Gaspe, Que., in 1905 and 1906. The Board of Management of the Marine Biological Station of Canada, created in 1898, was instrumental in the establishment of the permanent stations at St. Andrews, N.B., and Departure Bay, Nanaimo, B.C., in 1908. The sites were selected on the basis of ready access to fisheries and to abundant marine life and ready access to universities and sources of supplies. These two stations became the headquarters for the Canadian government's biological fisheries research in the Maritime Provinces and in British Columbia as administrative units with a large measure of autonomy. First active in 1908, their seventy-fifth anniversary was in 1983.

The government's action in 1898 was epoch making in two ways: it marked the beginning of long and effective support for fisheries research, and it established a Board of Management of eminent scientists, which evolved into the Biological Board of Canada (1912) and then the Fisheries Research Board of Canada (1937).

Management of Research by an Independent Scientific Board

The Board of Management of the Marine Biological Station, which held sway from 1898 to 1912, had nine members, all Canadian scientists eminent in the fisheries field, one (the chairman) representing the Department of Marine and Fisheries and the other eight from universities. The annual appropriation was administered by the Department with consequent restrictions and delays. Indeed, the resulting conflict between government administrators and the volunteer university scientists of the Board played its part in the pressure for a more independent

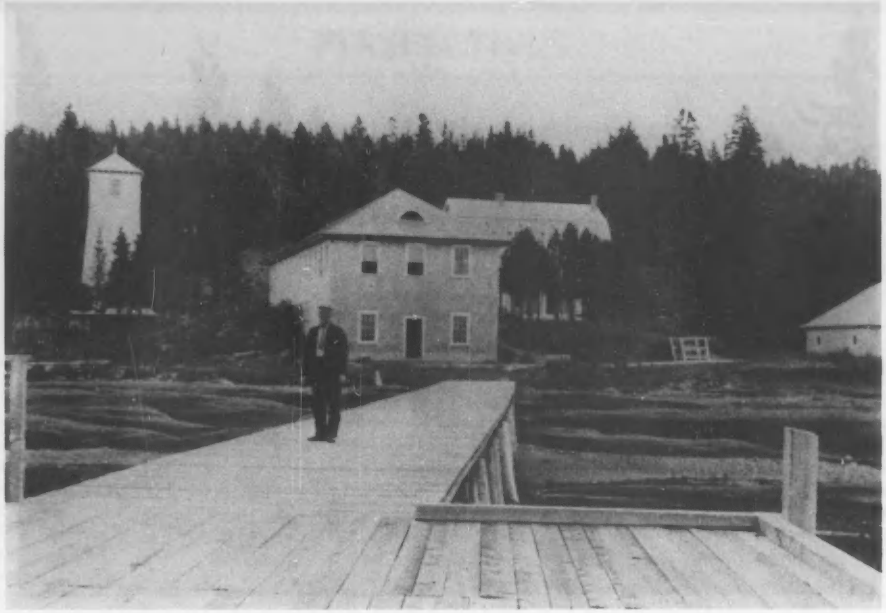

FIG. 2. The Atlantic Biological Station, St. Andrews, N.B., in 1909. To the left of the laboratory building is a tank tower to provide running salt water, behind it is the residence, and far right is part of a workshop building.

status. In 1912 this came through legislation establishing the Biological Board of Canada, which was given authority to manage its own appropriation through its own very small administration staff. This independence was continued when new legislation changed the Biological Board to the Fisheries Research Board in 1937, a change of name that reflected the greater emphasis placed by the Board from the twenties onward on research of direct practical importance to fisheries and the inclusion of technological as well as biological work in its program. Thus, from 1912 to 1973, when the Board was relieved of control over its programs and facilities and became an advisory body, the majority of its members were eminent university scientists serving in a voluntary capacity. The Board was responsible to the Minister concerned with fisheries and had members representing that Department and others representing the fishing industry, but it had control of its affairs, and in its counsels scientific opinion prevailed.

The excellence of the work of the two biological stations whose seventy-fifth anniversaries we celebrated in 1983 undoubtedly depended to a very large degree, as did that of other Board stations, on the independence and scientific integrity of the Board.

The Board's scientists knew that they worked for a body that appreciated scientific values, that their work was assessed mainly on its scientific quality, and that their own reputations and advancement were assured if they did good research. Morale was good and recruitment easy. The Board's scientific publications developed a reputation for excellence.

The Board could support long-term and fundamental research as well as immediate and applied. It could discourage waste of time on problems without prospect of scientific solution. The Board, with a majority of scientists but also with Departmental and industrial members, was able to maintain a reasonable balance between the long-term and the immediate and between the fundamental and the practical, knowing that all parts of the spectrum are important. The Board could protect against the tendency for pressure to be greatest for science that has already reached the applied stage as against more fundamental new science on which real progress depends.

The Board's administration was efficient because of relative freedom from red tape and because of quick access to authority. Scientific know-how could be applied quickly to such diverse problems as recruitment, procurement of equipment and supplies, and research vessel operations. Because of few steps between the stations and top authority, administrative decisions could be quick and frustrations kept to a minimum.

The independent Board was able to avoid the involvement with petty political patronage, which was common in government operations, especially in the Atlantic area, and which interfered with stable, rational administrative practices. Under the Board, recruitment and procurement were based only on merit.

One of the most favorable factors was a strong connection with university science at all levels of the Board's operations. In one way or another this has remained important to the present day.

Objective of Fisheries Research

From the very beginning the individuals and organizations proposing the establishment of the biological stations stressed the importance of marine biological research to fisheries. The avowed purpose of the stations was to provide the scientific knowledge on which to base the management and development of the fisheries. This, of course, is still their purpose. In seventy-five years our perspectives have changed and are still changing: every year brings new views of what research should be done. Some of the early research seems to us now to have little relevance to solution of fisheries problems, but early reports abound with declarations of faith that the marine biological research had great potential value to fisheries. Those who wrote those reports were, of course, right. The basis was being laid for more practical efforts to come.

Volunteer Investigators

At both stations from their establishment in 1908 to the mid-twenties the research was done mainly by volunteer investigators — university staff members and students who visited the stations during the summers and who usually received traveling and living expenses but never any more. Both stations had unpretentious residence facilities; both were to a degree isolated and at first used boat transportation to town for supplies, mail, etc. There was a communal atmosphere that was very strong and led many students into a career in fisheries science. My first acquaintance with salt water was at the St. Andrews station in 1924 and I well remember the stimulating atmosphere in the group of about 25 and the feeling of wonder, almost awe, at seeing so many and so varied marine creatures.

The volunteer investigators did very valuable work in providing background for more intensive fisheries research. Some of them were students but most of them were university staff members in a broad spectrum of biological subjects. Some were eminent; some were members, even chairmen, of the Board.

Their work was broadly exploratory: to learn what marine organisms were there, and how they lived. It included learning much about the life histories of commercial or potentially commercial species. It also included study of the oceanographic conditions and how they were related to the behavior and distribution of various species. The stations did not confine their work to their immediate vicinities but made excursions farther afield so that much was learned of fish, shellfish, and physical oceanography at a great distance, for example, on the Atlantic, in areas as far as the outer coast of Nova Scotia, the Gulf of St. Lawrence, and even the Strait of Belle Isle. Vessels and equipment were poor by modern standards and results often sketchy, but the general picture was revealed.

Practical fisheries problems were not neglected. Some of the knowledge about Pacific salmon runs, on which management is still based, was developed at that time. The nineteenth century naive faith in hatcheries and release of very young fry was questioned. It was shown, for example, that the lobser hatcheries of the day were worthless, and they were closed. I could give many other examples. The biological stations even started important research on processing fish, giving the first leads towards fast freezing. Suffice it to say that we who are still concerned with fisheries owe much to the early university volunteers whose only reward was the satisfaction of curiosity, during which they established for the Board a tradition of good science.

Expansion in the Twenties

In the twenties increasing recognition of the potential value of fisheries research led to pressure for greater efforts and more concentration on practical fisheries problems. As a result, the Board started to develop full-time scientific staffs at both biological stations. Research stations to deal with technological problems of fish processing and marketing were established on both coasts. Representation of the Department and of the fishing industry on the Board was strengthened. These developments eventually led to a new name, Fisheries Research Board, and a broader mandate in new legislation in 1937. At the biological stations new full-time staff concentrated their efforts on specific fisheries problems; university volunteers continued valuable research on their individual bents.

The expansion of biological research, which developed with the new full-time scientific staffs and which continued to grow for years to come, took somewhat different directions on the two coasts because of the very different conditions in the sea and in the fishing industry. Some items were common to both, notably increasing attention to oceanography, important to all fisheries.

On the Pacific coast, salmon contribute close to three quarters of the fishery's value and it was recognized, even by the fishermen, that salmon were in such demand and were so easily caught as they entered their rivers that the fishery could survive only if very strictly regulated to allow enough parent fish through to their spawning grounds. The recognition of the need for regulation which came from the salmon fishery was applied in the minds of the fishermen and processors to other species. On the Atlantic the fisheries depended mainly on species much harder to over-fish and there was then little public recognition of the need for regulation; that need has, of course, since been generally recognized.

The Pacific research program from the start concentrated on the basis for regulation of the fishery to assure adequate spawning "escapements" and on measures to maintain and increase salmon production in freshwater where there was the possibility of manipulating both the salmon and their environment. The Biological Station soon got into imaginative and effective research on the effects of pollution, on the means of guiding salmon past obstructions such as dams, on migratory patterns and capabilities of both adults and young, and on how to increase the capacity of the freshwater environment to produce young salmon. This concentration of effort on salmon was not, of course, allowed to prevent attention to the demands of other parts of the resource such as herring, groundfish, shellfish, marine mammals, and others.

On the Atlantic there was no part of the resource dominating the picture as did Pacific salmon, and research effort had to be broadly distributed among many sectors. Lobsters, groundfish, and herring had almost universal importance, but other resources were important locally: salmon, trout, scallops, oysters, clams, seaweeds, marine mammals, and others. Exploration and development of fishing gear, often in close cooperation with the Department or Provincial Governments, had much importance. In other words, there was a need for research to support fisheries development while at the same time keeping in mind the growing need for regulating some parts of the fishery to protect the resource.

The Great Depression of the Early Thirties

The expansion of research on fisheries problems which was started in the twenties was to an unfortunate degree nipped in the bud by the economic depression of the early thirties when funds for research were severely limited. Recruitment was halted and the skeleton year-round scientific staffs were denied adequate assistance. Some personnel were discharged; some were retained at reduced salaries. Field work suffered from lack of funds and equipment. The small scientific staff, of course, developed ideas and plans but suffered delays and frustrations.

The situation was aggravated at St. Andrews by a fire in 1932 that destroyed the laboratory building, much scientific material, and the whole of a valuable and growing library. Research was continued using residence space for office and laboratory work but under conditions made rigorous by the diversion of funds to rebuild part of the laboratory as a smaller, fireproof building. The station had neither space nor funds to support the same level of work by volunteers and this very valuable aspect of the university connection suffered a serious setback.

It must not be thought, however, that the work of either station stood still during the depression in the thirties. Progress continued in many of the lines mentioned in the preceding section. For example, on the Pacific the classic 8-yr comparison of natural and artificial propagation of sockeye at Cultus Lake reached a fruition that discouraged the further operation of all sockeye hatcheries, perhaps an over-reaction by the Department. Other salmon research in this period included studies of the migrations of all species, the start of intensive research on pink salmon production, and oceanographic studies in Alberni Inlet to learn the distribution and effects of pulpmill effluents. Research on pilchards and herring continued and intensive study of oyster culture was initiated, as well as exploratory investigations on clams, crabs, prawns, and many other subjects.

On the Atlantic, intensive research was initiated on the basis for management of the lobster fishery and for oyster culture, the latter involving establishment of a substation at Ellerslie, P.E.I., and undertaking direction of the Department's experimental oyster farming in the three Maritime provinces. Research on salmon and trout was continued and intensified. The groundfish fisheries, and sea fisheries generally, received attention, and the station participated actively in the work of the North American Council on Fishery Investigations, which coordinated research in the Northwest Atlantic on fisheries and oceanography by the United States, Canada, Newfoundland (then an independent Dominion), and France and which attempted to do in a small way what the International Council for the Exploration of the Sea was doing in the Northeast Atlantic.

The Second World War

As the thirties progressed, the financial difficulties of the Great Depression eased and a period of moderate growth ensued. The stations continued to lay the basis for fisheries management and to discover the oceanographic background. I believe that during this period the credibility of the Fisheries Research Board in the eyes of the Department, of the fishing industry, and of the public improved, but expansion of research suffered a further delay by the concentration of Canada's resources on the war effort. The government did not actively discourage research and, in fact, efforts were encouraged in two areas: one general and one particular.

In the first place, anything that would improve the supply of high-quality fish rated a moderately high priority. The nutritive value of the good proteins in fish created a demand for their shipment overseas, using the best techniques the Board's technological stations could recommend and rigid inspection, in which those stations also played a part. The result was a quality in the government-operated exports to Britain that has seldom been surpassed; the spinoff was the later use of some of the same techniques in expanding the domestic market. Export of luxury fish such as salmon and lobsters also helped with the foreign exchange needed to buy munitions.

More directly important to the war effort was cooperation by both stations with the Navy to develop techniques of hunting submarines. Echo-sounding methods for submarine detection depend for their effectiveness on a knowledge of the density structure of the water mass so that signals can be interpreted properly, and so that the effectiveness of echo-sounding, varying greatly at different times and places, can be understood and predicted. The Navy had the ships and the stations had oceanographers, and a close and very profitable relationship developed and lasted for many years. It is lucky for fisheries that there is a large overlap between the knowledge needed to hunt submarines and that needed to hunt fish.

Postwar Expansion

From my experience as one of the station Directors, on whose shoulders in those days fell major shares of long-term programming and of discussions with industry and department of what research projects were needed, I believe that it was in the forties that the balance of opinion of the Board's work tipped from a barely tolerant skepticism to a positive attitude. The stations' customers, whether government, fishermen, or the fishing industry, started pressing for more research than we could carry out. Combine this change with frustrations and hungers for resources during the depression and the war years, and with a more generous attitude of government when the war effort was over, and the result is, inevitably, expansion. It occurred in both stations, taking the form both of more adequate support for investigations already under way and of adventure into new areas. Because it would be futile to present them here in adequate perspective, the interested reader must seek details elsewhere; references are listed.

Two related phenomena deserve attention. Station scientific personnel became more and more closely engaged in discussions with the Department, fishermen, and the fishing industry on matters of domestic fisheries management and development and more and more involved as scientific advisors in international matters. Both these trends meant increasing pressure for research on practical problems and it is a wonder that as much attention to more fundamental research continued, as was the case. Such balance as was actually maintained between immediate and applied research, and more long-term and fundamental research prevailed simply because it was realized that the latter is essential to the success of the former. For a time the balance may have been tipped too much towards the application of science, and it is good to note that in recent years there has been a trend towards righting it by giving more attention to fundamental research.

The two major international commissions of the Northwest Atlantic and the North Pacific strongly influenced the programs of the two stations. Both commissions operated without their own research staffs and depended on research by the member countries, which meant dependence on the Board's Nanaimo Station in the Pacific and St. Andrews and St. John's stations in the Atlantic. The stations' reputations for sound scientific work became invaluable.

International Commission for the Northwest Atlantic Fisheries (ICNAF)

When 10 countries, in Washington in 1949, established

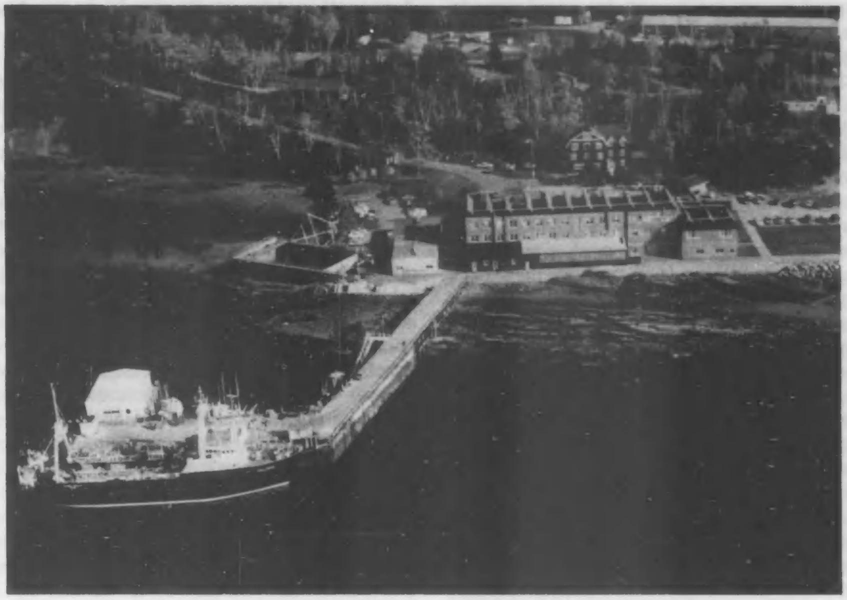

FIG. 3. An aerial view of the St. Andrews station in 1983 with an ocean-going research vessel at the wharf. Behind the main laboratory building with solar energy collectors on its roof is the former residence building now used for scientific working space and, on the hill above, further storage and working space in scattered frame buildings. The Huntsman Marine Laboratory campus is off the picture to the left.

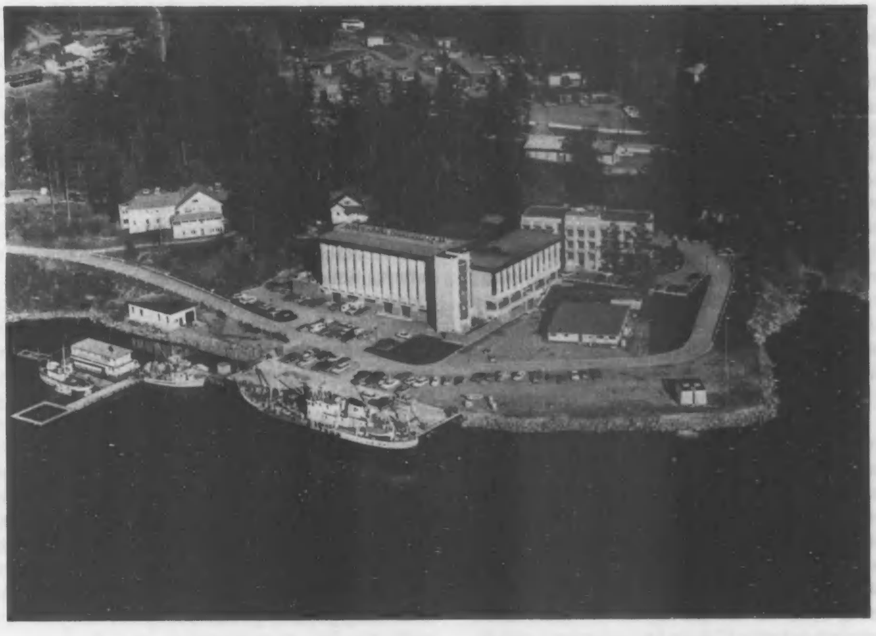

FIG. 4. A recent photograph of the Nanaimo station with the research vessel *G. B. Reed* at the wharf. The new wing completed in 1973 (center) is flanked by the older laboratory (with the sunshades) completed in 1949 on the site of the original frame building and by the former residence building (1928) now used for scientific working space.

ICNAF to recommend to member governments regulations to protect the fisheries resource in the Northwest Atlantic, it made heavy demands on the St. Andrews and St. John's stations of the Fisheries Research Board. St. Andrews hosted the second meeting of the Commission in 1952, provided temporary headquarters, and station personnel played a leading part in developing ICNAF headquarters activities, including the initiation of greatly improved fishery statistics, the first requirement of a regulatory commission.

In the early days of ICNAF it was hoped by the scientists of all countries that measures such as minimum-mesh sizes would suffice, but when serious overfishing developed with the advent of much greater fishing power from Europe (and new members of ICNAF), it became evident that the amount of fishing would have to be regulated. The Commission decided that catch quotas were more practical than attempting to regulate the amount of the very diverse fishing effort directly and that national allocations of quotas on each regulated stock would be necessary to prevent a mad scramble with each country trying to get as big a share as possible. The Commission's scientific committees were faced with recommending the total allowable catch (TAC) for each of some dozens of stocks that supported substantial international fisheries. ICNAF adopted this term for the quantity of fish that could be taken from each stock without long-term damage; it was determined by the Commission each year on the basis of recommendations by committees of scientists drawn from all member countries, but in Canadian waters the lion's share of the work was done by scientists of the St. Andrews and St. John's stations.

Necessary amendments to the Convention governing ICNAF came into force in December 1971. By the end of January 1972, ICNAF established TACs and national allocations for three large herring stocks, an all-time first in the management of multination fisheries. At the ICNAF annual meetings in June of 1972 and 1973 the same regulatory regime was extended to all important stocks in the Northwest Atlantic subject to international fishing. The battle to protect the stocks was joined but continued analyses showed that in 1975 and 1976 serious overfishing still went on even though TACs had been set close to the estimated sustainable yield. ICNAF adopted a policy of reducing the general level of TACs by about a third, thereby offsetting a number of adverse factors that could not be reduced to numbers, such as failures in enforcement, failure to report catches accurately, and inadequacies of the sampling data for sound calculations. This commonsense remedy did the trick; overfishing was stopped and stocks that had been seriously reduced started to recover. The better enforcement, which came with the extension of fisheries jurisdiction to 200 mi (322 km) and accompanying licensing, reinforced the action initiated by ICNAF. By and large the battle to maintain the resource was won.

The St. Andrews and St. John's stations made a very important contribution to the development of the ICNAF regime of regulation and its implementation in Canadian waters. Scientists from these stations continue to play an important part in the analyses that must continue in order to adjust the TACs as required. This needs sound applied science, which benefits from, and perhaps even requires, close association with research. The success of ICNAF and the regime it bequeathed to its successor (Northwest Atlantic Fishery Organization) outside the 200-mi zone and to the national administration inside depends on sound research and applied science.

International North Pacific Fisheries Commission (INPFC)

In 1953 a somewhat reluctant Japan entered into a treaty with United States and Canada designed to prevent damage by a vigorous and growing Japanese high-seas fishery to stocks of salmon, halibut, and herring on which North American fisheries depended. It provided that Japanese high-seas fishing for salmon should stay west of 175°W but required that joint research should determine the high-seas distribution of North American and Asiatic salmon stocks as a basis for adjustment of this limit, if necessary, to provide a "more equitable division" between the stocks from the two continents. Also, alone among all international fisheries treaties, it invoked the "abstention principle" under which nations are prohibited from entering fisheries that are already fully exploited, involving extensive analysis of the degree of utilization of the North American stocks of salmon, halibut, and herring. It set up INPFC to coordinate research by the three countries on the high-seas distribution of salmon stocks and to review the evidence that North American stocks of salmon, halibut, and herring continued to qualify for abstention by Japan.

The INPFC research program on salmon on the high seas was perhaps the most extensive international fisheries investigation ever undertaken. Canada's share became a major part of the research program of the Nanaimo station. The results were exciting and of great practical significance. In this program, standardized gill-netting showed the distribution and abundance of salmon over a wide area of the North Pacific and obtained samples for comparison with salmon taken inshore or in freshwater around the Pacific rim from Japan to the Columbia River. The characteristics of the various salmon stocks, their ages, scale patterns, meristic characters, physical proportions, parasites, and even some of their chemistry, were used to recognize them on the high seas. There were also extensive tagging and surveys of the oceanographic background.

Salmon were found to occur everywhere on the high seas north of the 14°C isotherm and in some places, e.g. the centre of the Gulf of Alaska, in considerable abundance. The various river stocks intermingled over wide areas but only salmon with appropriate characteristics returned to the rivers and their approaches. Two sockeye stocks were recognizable throughout their lives from seaward migrants (smolts) to returning spawners: Bristol Bay by a parasite and Rivers Inlet by a unique scale pattern; although mixed on the high seas over some 30° of longitude, inshore sampling did not reveal any returning to the wrong area. In other words, salmon are widely distributed and mixed on the high seas but "home" to their rivers of origin. The migrations sometimes take them thousands of miles. In some cases, from tagging on the high seas to capture inshore, individuals apparently traveled at three-quarters their sustainable speed.

This program provided convincing evidence that stocks of salmon have their own inherited migratory patterns on the high seas. Other work by the station showed that young salmon in freshwater also have inherited migratory patterns differing greatly from stock to stock and that these movements in freshwater, as in the ocean, demonstrate ability for directional swimming guided by some cues other than chemical or physical gradients. This demonstration opens the way to many conjectures, which in turn suggest that salmon, although spectacular, are not unique in this regard. Many seasonal migrations of marine fish suggest a similar ability. In all cases such migratory patterns have apparent survival value to the stocks.

Thus, the INPFC research program, although stimulated by a treaty requirement concerning international controversy, turned out to be valuable fundamental research with possible broad applicability.

The Developing Research Programs of the Stations

So much space has been given to the two international commissions, ICNAF and INPFC, not only because of their importance to Canadian fisheries but also because they provide excellent examples of the satisfaction by the stations of urgent needs of the government. In both cases the research was given a suitably high priority. In both cases the performance could not have been nearly so good if the stations had not already developed competent staffs in appropriate fields and if the stations had not readily adjusted programs to meet the new needs. In both cases the stations received some additional financial support but depended greatly on resources, human, physical, and financial, already on hand. In both cases some scientific personnel felt that the new work interrupted more fundamental research, but in both cases all came to realize the general value of the work for the commissions and the indirect support given to research along many avenues. In both cases the stations' scientists were brought into close and effective consultation with Departmental and industry personnel. In other words, these are good examples of how well the Fisheries Research Board stations could adjust programs to meet urgent national needs, carry out effective scientific work, and communicate its results fully and promptly.

There are too many other examples to attempt to list or comment on them. The stations' programs have, in fact, been developed to meet needs of government and of the fishing industry: to solve problems that are sometimes formulated by those "customers" of the stations but are sometimes necessarily formulated by the research scientists who recognize first what the real needs are. This latter factor is important, experience having shown that the greatest government and industry pressure is often for research on problems on which a great deal is already known and even in use. Effective programming must include attacks on problems first recognized by the scientists themselves. Of course, government must, in consultation with both industry and research, decide the fields in which the stations work, but effective programming within those fields depends on a continuing, competent, and devoted body of research workers dedicated to the solution of fisheries problems, long term as well as short. It was encouraging to note in discussion with station personnel on both coasts a trend toward fundamental research, sometimes exploring new fields, sometimes providing a sounder basis for solving practical problems on which some progress has already been made.

Only a dedicated continuing scientific staff can handle the difficult problem of keeping the balance between immediate applied research and the broader, deeper "fundamental" research on which real progress depends. It is, of course, possible to contract out some short-term problems to consultants or universities, but only a strong continuing research staff can properly direct the more important long-term research. That continuing staff, however, profits for breadth of vision from a strong university connection.

The Changing University Connection

When support for university volunteer scientists suffered from a shortage of funds in the Great Depression of the thirties, exacerbated at the St. Andrews station by a disastrous fire, it did not, of course, destroy the university connection entirely. The Board itself continued to be mainly university scientists, and the stations employed increasing numbers of students, and sometimes university staff, as the research program grew in the forties and fifties. This mainly seasonal support often suited both the universities and the Board, combining financial and intellectual cooperation. To this day, university staff and graduate students find it profitable to work during the summers on subjects important to the stations and there are undergraduate student employment programs to meet this need.

At an institutional level the St. Andrews station assisted in the development of the Huntsman Marine Laboratory, which, although mainly a consortium of universities, has representation from the fisheries departments of both the Federal and New Brunswick governments among its Directors. In its early stages, starting in 1970, the station assisted the Huntsman Marine Laboratory with temporary laboratory space, which had been designated for university use, and helped the laboratory develop its own campus adjacent to the station. The relationship has been mutually beneficial and is thriving, providing field courses for students and facilities for research by university scientists. On the Pacific coast a consortium of universities established a laboratory at a greater distance, but the Nanaimo station has developed cooperative programs with British Columbia universities and Malaspina College involving undergraduate and postgraduate support and exchange of scientists. On both coasts station, laboratory, and vessel facilities are sometimes used by universities to their mutual advantage.

Demise of the Fisheries Research Board

In 1973 the Fisheries Research Board was relieved of administrative authority over its facilities and programs and became a purely advisory body. A few years later it disappeared altogether. The stations lost much of their autonomy and identity as administrative units. Both were integrated into the Department as parts of the organizations responsible to the Regional Directors, placing some additional administrative steps between the stations and the top authority in Ottawa. Delays and inefficiencies resulted, red tape and frustrations increased, and there was loss of morale. Research activities are no longer responsible to a scientific board and through it to top administration in Ottawa; instead, they are responsible to top authority through less scientifically qualified local authorities. The Fisheries Research Board is gone and with it many of the advantages that made it one of the world's most successful research agencies in its field.

One wonders why such a change was made. One of the reasons cited was lack of communication between research and other departmental activities, but in my experience as Station Director on the one hand, and as Deputy Minister on the other, this explanation has no validity. I recall no cases in which advice was not made readily available on small matters or large; I do recall many cases in which research plans were quickly modified to get answers to urgent questions. There were no failures in communication that could not be overcome by consultation on either an ad hoc or a formalized basis. One is tempted to blame the common tendency of the central agencies of government to encourage uniformity in administrative arrangements and controls and to distrust the unusual and the poorly understood, even when outstandingly successful.

It is too soon to assess the effects of this major change on fisheries research in Canada. Many of the benefits of the Fisheries Research Board regime continue because of the persistence of dedicated people; the new regime may be modified to preserve them further. Let us hope that means may be found to provide better communication between the stations and top policy making and to avoid the dangers of scattering research efforts and personnel so much among nonscientific activities as to lose the very real advantages of continuing research in large and able groups of dedicated scientists. Perhaps the recently established Fisheries and Oceans Research Advisory Council (FORAC), which in a sense assumed the advisory functions of the last years of the Fisheries Research Board, will be able to guide us out of the morass to clearer, firmer ground for future research.

The Seventy-Fifth Anniversary and the Future

Casting off all thoughts of changing status and loss of identity, both stations celebrated their seventy-fifth anniversary in 1983. They still have strong and well-justified feelings of pride in past performance and of hope for the future. The need for improving the scientific basis for fisheries management and development is still there. As we learn more we reveal more leads for promising research, sometimes opening new fields, sometimes improving the fundamental understanding of old. It is still necessary to keep a good balance between the short term and the long term and between the applied and the fundamental. It seems unthinkable that means would not be found for improving communication between research and administration at top as well as local levels and for maintaining the vitality of important research centers such as St. Andrews and Nanaimo.

The stations' physical assets have never been better: well-equipped laboratories and use of a growing fleet of good research vessels. More important, the new generation of scientists are very able indeed and inevitably become dedicated to the intriguing world of fisheries science with its great diversity and challenge.

Let us look forward to a hundredth anniversary for the stations as honorable as their seventy-fifth.

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NEEDLER, A. W. H. 1958. Fisheries Research Board of Canada Biological Station, Nanaimo, B.C., 1908–1958. J. Fish. Res. Board Can. 15: 759–777.

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BOOK REVIEWS / COMPTES RENDUS

Canadian Tidal Manual. *Prepared by W. D. Forrester, Department of Fisheries and Oceans, Canadian Hydrographic Service, Ottawa, Ont. 1983. 138 p. $20 (Canada); $24 (other countries).*

This manual was produced under contract to the Canadian Hydrographic Service so that they could have both a text for their hydrographic surveying courses and a field manual for survey parties. Hence, Forrester was forced to walk a fine line between theory and practice, and although the book is not all-encompassing, it will be of interest to anyone who is involved with the practical measurement of tides and currents.

The book is in two sections: the first deals with physical oceanography and the theory of the tides and the second deals with the practical aspects of installing gauges, documentation, with the various types of tide gauges, and the methods of measuring currents. It is well illustrated and some of the photographs alone, especially that of the wake behind Turret Island, B.C., and those of the various tidal bores, are worth the price of the book.

The theoretical section is a concise summary of the physical oceanography associated with tides and contains excellent descriptions of inertial oscillations, internal waves, amphidromic systems, the equilibrium tide, and meteorological forcing. In all cases the explanations are clear and the use of mathematics is kept to an absolute minimum. Even if the mathematics must be skipped, the explanations are clear enough to follow. There are plenty of caveats about the differences between the equilibrium tide and the measured water level or current, and the relationships between the three are carefully explained.

It is fortunate that all Canadian hydrographers are based in oceanographic research institutes. This means that they have a ready source of advice and access to the most up-to-date research. Forrester has relied on this and has not clearly put all of the oceanography into a proper context, so that an unsuspecting neophyte could easily get the impression that Forrester has written a comprehensive work on the subject. Of course, all of the topics are the subject of active research and the explanations are fairly superficial. This deficiency is easily overcome in hydrographic courses by a good instructor, but there is a more general audience whose only source of immediate reference will be this book. It would not have taken very much space to place things in the proper context and to have provided some general references in appropriate places in the text.

A careful reading of the theoretical section will provide an adequate grounding in the necessary aspects of tidal theory, harmonic analysis, and the various types of forcing, apart from the tide, which cause the motion of large bodies of water. This grounding will be without jargon and unmathematical but will provide all that is necessary for the field hydrographer, engineer, or biologist who must make, or interpret, tidal measurements in order to get on with his work or who wants to be able to talk intelligently to a physical oceanographer about problems related to tides or currents.

The second section of the book is the one that will be of most use to the field hydrographer. Chapter 6 deals with the establishment of temporary gauges, the different types of gauge, site selection, benchmarks, and leveling. Chapter 7 deals with operating the gauges, documentation, and sounding reduction. It is for these two chapters that most people would purchase the book, and although they deal primarily with CHS practice, they should be of use to anyone who wants to install a water level gauge. These chapters are general enough that they will not go out of date quickly, and yet, armed with this book and the instruction manual for a particular gauge, there is enough information here that anyone could install and operate a gauge so that it would give accurate, documented data. The theoretical section should have provided enough background that the data are also useful.

The final chapter of the book deals with current measurements and this is the most unbalanced of the chapters. Current measurement, in general, is the subject of much controversy and active research. Forester has dealt generically with all of the various methods and has devoted approximately equal space to current meters, current crosses, drift poles, drogues, continuity, hydraulics, electromagnetic induction, and geostrophic methods. It is here that the lack of context is most apparent. There are orders-of-magnitude difference in the sophistication of all of these methods, but all are used and are useful for very different reasons, none of which is made particularly clear. Again, the Canadian hydrographer would not find any difficulty, since he has a ready source of advice, but a more general audience could find some of the discussion very unsatisfactory. This problem could be simply remedied at the cost of a couple of additional paragraphs of text and some references.

I would have preferred to see Forrester write a huge tome with all aspects of tidal theory and practice combined into one huge reference work, but this would easily run to more than one thousand pages and would not have accomplished the aim of providing a practical handbook for field hydrographers. Within the limits imposed, this is an excellent work — it is short, concise, easily understood, and deals with all of the necessary topics. Anyone who has read this far in the review should seriously consider purchasing a copy.

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(R509)

Écologie du plancton des eaux continentales. Collection d'écologie 16. *R. Pourriot, J. Capblancq, P. Champ et J.-A. Meyer. Masson Edit., Paris. 1982. 198 p. Fr 184.*

Réaliser une synthèse la plus complète possible sur le phytoplancton et le zooplancton des eaux douces était une entreprise difficile. Les quatre auteurs de ce livre ont cependent relevé un défi, tout en étant conscients eux-mêmes des critiques qu'on peut leur faire sur le développement à donner à tel ou tel aspect d'un sujet aussi complexe.

Le premier chapitre traite des communautés phytoplanctoniques, des bases écophysiologiques de la production primaire et des variations de cette production dans les milieux naturels. Les variations avec la profondeur nous semblent particulièrement bien exposées. Par contre, la composition spécifique du phytoplancton est très brièvement traitée.

Le deuxième chapitre a trait aux consommateurs et à la production secondaire. L'alimentation et les mécanismes fondamentaux de transferts de matières et d'énergie sont exposés de façon très complète. Les sections biologie et démographie, méthodes d'estimations de la production secondaire, résument bien les diverses méthodes utilisées dans ce domaine mais ne mettent pas assez en évidence les résultats obtenus. Dans la présentation de la structure des communautés planctoniques, nous aurions souhaité que les auteurs discutent des théories développées par Andersen, Kerfoot et De Moh, Lewis, Neill et Peacock, Sprules, lors du symposium de l'American Society of Limnology and Oceanography (Kerfoot 1980).

Le troisième chapitre donne une excellent définition du concept de stratégies adaptatives et des exemples de stratégies développées par le zooplancton pour répondre aux pressions sélectives de la prédation et de la compétition. On peut cependant aussi regretter ici que les résultats des chercheurs cités plus haut n'aient pas été discutés.

Le quatrième chapitre traite des modèles de simulation de la dynamique du plancton. La structure des modèles (variables d'état, fonctions de forçage, variables d'entrée, paramètres, constantes, etc.) est clairement décrite. L'auteur présente quelques modèles simples de simulation en expliquant la signification écologique des termes des équations et les algorithmes utilisés, ce qui permet de démystifier auprès des non-initiés l'utilisation des techniques informatiques. Il décrit la suite rigoureuse des étapes à franchir pour tester un modèle de simulation (sensibilité, calibration et validation) et termine par une excellente synthèse sur le devenir des modèles.

La bibliographie citée dans les quatre chapitres est abondante (216, 266, 162 et 111 références). Si l'oubli de quelques auteurs nord-américains a été souligné, nous devons par contre signaler l'utilisation d'une abondante littérature européenne.

En conclusion, nous pensons que ce petit livre constitue une excellente initiation à l'écologie du plancton des eaux continentales.

KERFOOT, W. C. 1980. Evolution and ecology of zooplancton communities. Special symposium. Ann. Soc. Limnol. Oceanogr. 13: 625–741.

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Opisthobranchia des Mittelmeeres. Nudibranchia und Saccoglossa. *L. Schmekel and A. Portman. Springer-Verlag, Berlin. 1982. 410 p., 36 plates (18 in color), 122 figures. Approximately $163 (U.S.).*

This lavishly illustrated volume constitutes No. 40 in the series on the fauna and flora of the Bay of Naples, Monographs of the Zoological Station of Naples. Whereas the majority of the text is in German, all of the species descriptions are repeated in English at sufficient length to enable identification when used in concert with the fine line drawings. More than 80 of the 127 species of nudibranchs and saccoglossids are meticulously illustrated by I. Richter whose work has graced this series before.

Tabulations of the classification from ordinal to specific rank are followed by keys first to superfamilies and tribes and then to families and genera. These are not all, unfortunately, translated, and the keys precede the introduction to general anatomy and have no references to the copious illustrations. More than 250 detailed pages of descriptions follow, complete with additional information on distribution, life history, and food. Whereas the volume is clearly based on the Mediterranean fauna, it provides a fundamental tool for malacologists, and there are some West Atlantic species that will be encountered by Canadians working Florida and the Caribbean.

It is encouraging to see the perpetuation of these classic series by organizations such as the sponsors of this volume, the Ray Society, and others (such as the Linnaean Society and Freshwater Biological Associations in Britain) that produce simpler illustrated guides to invertebrates. Until recently, the best Canadian efforts in the aquatic field were perhaps guides to fish, but the Entomological Society of Canada has entered the field with the recent Monograph 27, Volume 1, of the Manual of Nearctic Diptera. This venture, supported by the Department of Supply and Services, is being closely studied by the Canadian Society of Zoologists and its proposal for a Biological Survey of Canada. A reinstated Canadian Marine Fauna series combining the best efforts of government, academic, industrial, and private support would give focus to the existing taxonomic expertise in the country, encourage more participation, and provide a vital tool for environmental assessment projects as well as an inventory of a neglected national treasure. Treated with the esthetic appeal of the volume under review, parochial pride could be harnessed to valuable scientific and aristic creativity.

The Opisthobranchia volume will be a required tool for malacologists and will find a market among biologists who enjoy fine books, but it is an unashamedly specialized work that will be housed largely in libraries.

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BOOKS RECEIVED / LIVRES REÇUS

August–September / août–septembre 1983

Computer Management of Fish Health Problems in Hatcheries. *G. E. Hoskins, C. J. West, and A. E. Kling. Canadian Special Publication of Fisheries and Aquatic Sciences 68. Government of Canada, Department of Fisheries and Oceans, Ottawa, Ont. 1983. 42 p. $5.00 (Canada); $6.00 (other countries).* Following diagnosis of an infectious disease, the computer program described here will assist in selection of the appropriate treatment procedure, perform all the necessary calculations, and outline the method of application. The program is written in the "Applesoft" version of BASIC and for a limited time is available on a 5¼-in. floppy disk. $40.00 (Canada); $48 (other countries). [R517]

Aquatic Life in the John G. Shedd Aquarium. *Shedd Aquarium Society, Chicago, IL. 1983. 272 p.* Included in this book is a "A guide to exhibit animals in the John G. Shedd Aquarium." The book is well illustrated with many photographs, almost a third in full color. There is an interesting accompanying text about each group of animals, largely fish, but other phyla are also included. The treatment is worldwide. [R518]

Fishes of Pennsylvania and the Northeastern United States. *Edwin L. Cooper. The Pennsylvania State University Press, University Park (Penn) and London. 1983. 243 p. $27.50 (U.S.).* This book summarizes information obtained over the last couple of decades. It is a detailed scientific survey of all fishes of Pennsylvania. The major portion of the volume consists of illustrated keys to the identification of about 190 species of fishes. Spot distribution maps, black and white photographs, and line drawings are included. [R519]

Biologia Acuatica No. 4: Demografia del Pejerrey *Basilichthys bonariensis bonariencis* (Pisces Atherinidae) en el Embalse Rio Tercero, Cordoba. *Lauce R. Freyre, Lucila C. Protogino, and Juan M. Iwoszkiw. Contribucion Cientifica 227 del Instituto de Limnologia "Dr. Raul Adolfo Ringuelet," La Plata, Argentina. 1983. 39 p. $5.00 (U.S.) (includes postage).* A population study including a detailed description of the fishing arts using the FAO (Food and Agriculture Organization of the United Nations) rules. Available from Lic. Hugo L. Lopez, Instituto de Limnologia, Casilla de Correo, 55, 1923 Berisso, Argentina. [R520]

Fish Stock Assessment: A Manual of Basic Methods. *FAO/Wiley Series on Food and Agriculture, Volume 1. J. A. Gulland. John Wiley & Sons, New York, NY. 1983. 223 p. $34.95 (U.S.).* This, the first in a series of practical books, describes techniques used in assessing fish stocks worldwide, in evaluating the effect of fishing on the stocks, and the likely impact of different policies for developing and managing fisheries. Especially valuable for scientists in fishery research and students in fishery science and marine ecology. [R521]

From Leadline to Laser. Centennial Conference of the Canadian Hydrographic Service. *Canadian Hydrographic Service/Canadian Hydrographic Association. Canadian Special Publication of Fisheries and Aquatic Sciences 67. 1983. 223 p. $12.00 (Canada); $14.40 (other countries).* These proceedings review various aspects of the history of hydrography in Canada as well as covering a wide range of topics from around the world. [R522]

Fibre Ropes for Fishing Gear. *Gerhard Klust. An FAO Fishing Manual. Fishing News Books Ltd., Farnham, Surrey, England. 1983. xvi + 200 p. £9.50.* This manual will help fishermen and net makers achieve optimum selection and utilization of ropes. It provides information on materials, construction, properties, treatment of the main types of ropes, as well as guidance for proper selection and application for different types of fishing gear. [R523]

ANNOUNCEMENTS / AVIS

Nineteenth Canadian Symposium on Water Pollution Research

Thursday, February 23, 1984

The Wastewater Technology Centre (WTC) and the National Water Research Institute (NWRI) will host the 19th Canadian Symposium on Water Pollution Research. The meeting will be held at the Canada Centre for Inland Waters in Burlington, Ontario.

The purpose of the Symposium is to provide a forum for discussion of recent research investigations carried out in Canada in the field of water pollution and its impact on the aquatic environment. The Symposium will be organized in two current sessions: (1) Water Pollution Control Technology and (2) Impact of Pollutants on Aquatic Ecosystems.

Papers will be published in the *Water Pollution Research Journal of Canada*. The acceptance of an abstract for the presentation of a paper at the meeting does not necessarily imply that the finished manuscript will be acceptable for publication in the *Journal*. Finished papers will be reviewed by the Editorial Board before final acceptance for publication.

For additional information including preregistration material and the program, please contact Dr B. E. Jank, Chairman, Session 1, Wastewater Technology Centre, Canada Centre for Inland Waters, P.O. Box 5050, 867 Lakeshore Road, Burlington, Ont. L7R 4A6; Dr J. M. Barica, Chairman, Session 2, National Water Research Institute, Canada Centre for Inland Waters, P.O. Box 5050, 867 Lakeshore Road, Burlington, Ont. L7R 4A6

Dix-neuvième symposium canadien de la recherche sur la pollution de l'eau

Jeudi 23 février 1984

Le Centre technique des eaux usées (CTEU) et l'Institut national des recherches sur l'eau (INRE) seront les hôtes du 19e Symposium de la recherche sur la pollution de l'eau. La réunion aura lieu au Centre canadien des eaux intérieures à Burlington (Ontario).

Le Symposium vise à servir de forum aux discussions sur les travaux de recherche effectués récemment au Canada dans le domaine de la pollution de l'eau et sur son impact sur l'environnement aquatique. Le Symposium comprendra deux ateliers: (1) techniques de lutte contre la pollution de l'eau et (2) impact des polluants sur les écosystèmes aquatiques.

Les documents retenus paraîtront dans le *Water Pollution Research Journal of Canada*. Le fait d'accepter un résumé pour la présentation d'un document à la réunion ne suppose pas nécessairement que la version finale paraîtra dans le *Journal*. La dernière version de tout document présenté sera révisée par la Rédaction avant que l'on n'autorise finalement sa publication.

Pour de plus amples renseignements, y compris les documents fournis avant l'inscription et le programme, prière de communiquer avec Dr B. E. Jank, Président, Atelier 1, Centre technique des eaux usées, Centre canadien des eaux intérieures, B.P. 5050, 867, Chemin Lakeshore, Burlington (Ont.) L7R 4A6; Dr J. M. Barica, Président, Atelier 2, Institut national des recherches sur l'eau, Centre canadien des eaux intérieures, B.P. 5050, 867, Chemin Lakeshore, Burlington (Ont.) L7R 4A6.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Articles

Utilization of phytoplankton by zooplankton during the spring bloom in a Nova Scotia inlet **R. J. Conover and P. Mayzaud**

Distribution of digestive enzymes in zooplankton during the spring bloom in a Nova Scotia inlet **P. Mayzaud and R. J. Conover**

An integration of forest and lake fertilization: transport and transformations of fertilizer elements **C. J. Perrin, K. S. Shortreed, and J. G. Stockner**

Deposition of fine and coarse sand in an open-work gravel bed **P. A. Carling**

Resource management biology for the edible kelp *Cymathere triplicata* **W. G. Roland**

Recent colonization of a major salmon-producing lake in British Columbia by Pacific lamprey (*Lampetra tridentata*) **S. P. Farlinger and R. J. Beamish**

Distributions of ferrous iron and sulfide in an anoxic hypolimnion **R. B. Cook**

Ichthyoplankton associated with a warm core ring off the Scotian Shelf **J. S. Wroblewski and J. Cheney**

Development of larvae of the saffron cod, *Eleginus gracilis*, with comments on the identification of gadid larvae in Pacific and arctic waters contiguous to Canada and Alaska **J. R. Dunn and B. M. Vinter**

Spawning site water chemistry and lake trout (*Salvelinus namaycush*) sac fry survival during spring snowmelt **J. M. Gunn and W. Keller**

Divergent structure in fish taxocenes of north temperate streams **R. Mahon**

Contribution of particulate phosphorus (>250 μm) to the total phosphorus pool in lake water **E. E. Prepas and J. Vickery**

Behavioral response of blacknose dace (*Rhinichthys atratulus*) to varying densities of predatory creek chub (*Semotilus atromaculatus*) **D. F. Fraser and E. E. Emmons**

Characterization of protease from the myxosporean salmon parasite, *Hennaguya salminicola* **E. Bilinski, N. P. Boyce, R. E. E. Jonas, and M. D. Peters**

Notes

Fyke net catches as indices of the abundance of brook trout, *Salvelinus fontinalis*, and Atlantic salmon, *Salmo salar* **P. M. Ryan**

An improved flow-through respirometer for aquatic macroinvertebrate bioenergetic research **F. J. Wrona and R. W. Davies**

Ethanol fractionation of lacustrine colloidal fibrils **B. K. Burnison and G. G. Leppard**

Incubation of the eggs of Atlantic salmon, *Salmo salar*, at low temperatures **T. G. Heggberget and J. C. Wallace**

Book reviews/Comptes rendus

Research on fish and wildlife habitat (W. T. Mason Jr., technical editor) **G. A. Vigers**

Theory and management of tropical fisheries (edited by D. Pauly and G. I. Murphy) **W. G. Doubleday**

Books received/Livres reçus
Corrections to recent publications/Corrections sur récents publications

Guide for Authors

Introduction

We welcome manuscripts reporting significant new information in fisheries and aquatic sciences. Manuscripts may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems and cover numerous disciplines including biology and ecology of marine and freshwater organisms, physiology, toxicology, genetics, limnology, oceanography, economics, disease, and management.

Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented. Preference will be given to those whose experimental results emphasize causal mechanisms underlying observed phenomena rather than pure description and fact. Manuscripts should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. Their novelty must relate to more than the particular (a certain year, place, taxon, chemical compound) and their contribution to science must clearly be beyond the confirmatory state.

Manuscripts submitted should be as comprehensive as possible; research fragments are generally unacceptable. If a single paper cannot be produced, then closely related papers should be cross-referenced and submitted together. The paper should not be submitted or accepted for publication elsewhere.

The *Journal* considers the following types of contributions:

Articles: Studies of broad scope that are original contributions to science.

Notes: Reports of significant new knowledge arising from problems with narrow limits or important findings that warrant immediate publication before broader studies are complete. Notes should occupy no more than 3 printed (9 manuscript) pages.

Reviews: Detailed critical appraisals of broad areas of investigation, particularly those that have developed rapidly in recent years.

Perspectives: Essays of opinion or hypothesis on aquatic science of concern to the professional and layman. References are desirable; informal style is welcome.

Comments: Opinion on topics recently discussed in the *Journal*; preferred maximum length, 500 words.

Manuscript Submission

Submit manuscripts in triplicate to the Editor, accompanied by a covering letter that (1) states the main points and significance of the work, (2) accepts the mandatory page charge, (3) suggests potential referees, and (4) identifies other manuscripts containing the same or similar information. Original typescripts and figures (except halftones) are best retained by the author until requested.

Each manuscript is normally submitted to two referees for appraisal before final evaluation by an editor. However, the Editor will return unreviewed those manuscripts that do not fall within the *Journal*'s editorial policy or scope.

Editorial Practices

The *Council of Biology Editors Style Manual* (5th ed., CBE, 9650 Rockville Pike, Bethesda, MD 20814) is used as the authority in matters of form. The standards for spelling are either *Webster's Third International Dictionary* or the *Oxford English Dictionary* and *le Grand Larousse Encyclopédique*. Authors are responsible for consistency in spelling. Titles of periodicals are abbreviated as in *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103). The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (4th ed. 1980), Spec. Publ. No. 12, American Fisheries Society. All measurements must be metric, use SI symbols in most instances (exceptions noted in editorial in *Journal*, Vol. 41, No. 1), and adhere to the *Canadian Metric Practice Guide* CAN3-Z234.1-79 (Canadian Standards Association, 178 Rexdale Boulevard, Rexdale, Ont. M9W 1R3).

Series titles should be avoided. An abstract is required for all manuscripts and should state concisely, in up to 175 words, what was done, found, and concluded.

Proofs are sent to the author, who is responsible for correcting errors in typesetting. *Alterations to the content must be avoided.*

Fifty reprints are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent with the proofs).

Preparation of Manuscripts

General Guidelines

Movement of manuscripts through review channels and the editorial office is greatly expedited if manuscripts are prepared in *Journal* style and format. When in doubt about specific details, consult a current issue of the *Journal*. General guidelines follow.

Type the manuscript on white paper, preferably 21.5 × 28 cm (8.5 × 11 in.), on only one side of the page. If possible, use paper with lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Type only the title, authors' names and affiliations, and related footnotes on the first page. Number all pages beginning with the title page, including those for tables and captions for illustrations.

Double-space all parts of the manuscript, including tables, captions for tables and figures, footnotes, and the reference list. Underline only material that is to be printed in italics.

Do not use all capitals anywhere in the manuscript. In tables and headings, capitalize the first letter of each word.

Use the name-and-year system for literature citations.

Checklist for Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately in a data or manuscript report or at a data repository?

If statistical analysis is included, is it subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report? Does the *abstract* give the essentials of the new knowledge? Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of *materials and methods* limited to what scientists need to understand the design of the study and to judge the adequacy of the data? Are generalizations from the *results* supported by the data provided? Are findings distinguished from inferences? Is the *discussion* limited to interpretation and significance of the findings?

The most common technical problems in submitted manuscripts are listed below. Authors can hasten the processing of their papers if they pay attention to these points during manuscript preparation.

1) Insert bibliographic strip before the abstract (Authors, date, title, Can. J. Fish. Aquat. Sci.).

2) Limit abstract to one paragraph of about 175 words.

3) Double-space all elements of the manuscript, including references, table captions, and figure legends.

4) Avoid exclusive use of capitals everywhere in the manuscript, including headings, table captions, and figure legends.

5) Underline only Latin names of organisms and certain statistical and mathematical notation to indicate italics.

6) Use correct SI symbols for units of measure in figures, tables, and text. Place a zero before the decimal for numbers less than unity.

7) Avoid ambiguous forms such as $\mathrm{g\ C/m^2/d}$; use $\mathrm{g\ C{\cdot}m^{-2}{\cdot}d^{-1}}$.

8) Identify test used to test statistical significance and give probability value. No reference is needed for common statistical tests.

9) In the text generalize from tables and figures; avoid repeating all of the details. Be sure each table and figure can stand on its own and is referred to in the text in numerical order. The captions should explain the purpose of the table or figure.

10) Include acknowledgments section at manuscript stage, not when galley proofs arrive.

11) Provide the person's initials and mailing address when referring to personal communications.

12) Delete unnecessary references that do not apply directly to the problem.

13) Check references carefully against text citations and vice versa to ensure exact correspondence. Provide an availability statement for less easily retrieved material, e.g. available from Department of Economics, Simon Fraser University, Burnaby, B.C. V5A 1S6.

14) Delete commas between name and date in citations such as (Smith 1900) and do not underline "et al."

15) Replace 10^n in table headings and figure axes with appropriate SI prefixes or use words (e.g. thousands).

16) Photocopies of figures, except halftones, are appropriate for review purposes. Send photographic prints of figures, or originals if they do not exceed 21.5 × 28 cm, on request for publication. Use the same type of lettering throughout if possible.

Parts of the Manuscript

Organization

Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in presentation of manuscripts.

See that everything in each section is relevant to the heading, and everything in each paragraph to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

Title

Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (1) it allows the reader to judge whether or not the article is of potential interest and (2) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximum amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g. X ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to …" or "Investigations on …" Good titles greatly assist scientists and librarians in using scientific literature and aid indexers preparing titles for keyword indexes.

Abstract

The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as "... is discussed" or "... was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents.

Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

Materials and Methods

Materials and Methods provides the framework for getting answers to the questions concerned in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine ... we ..." If the section is long, consider using subheadings corresponding to headings for the findings.

Results

Limit the results to answers to the questions posed in the purpose of the work, and digest them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made and so avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the text what is clear from the titles. Material supplementary to the text can be archived in the report literature or a recognized data depository and referenced in the text.

Discussion

Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

Acknowledgments

We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence. Nearly every manuscript submitted to the *Journal* contains errors in the references.

Tables

Tables are used to present repetitive data and should be as economical of space as possible.

Design tables to fit within either a column or page of the *Journal*.

Type each on a separate page and number with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Table captions should be succinct and identify the purpose of the table sufficiently well to allow the table to stand on its own.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines.

Figures

Provide photographic reproductions or the original artwork (no larger than 21.5 × 28 cm) of each illustration. If submitting photographs, type the author's name and figure name on a strip of paper and fasten to the back of the print. Do not write on the illustration itself. Provide two photocopies of line illustrations and two sets of any photographs for review purposes.

Design figures to fit a 1-, 2-, or 3-column width in the *Journal* and ensure that all lettering, numerals, and symbols are legible, neat, and at least 1.5 mm high when reduced. Figures should not be mounted, stapled, or clipped. When possible, figures should be grouped and be done with the same or similar type of lettering.

Type legends in succession on a separate page. Add bar scales to maps, photomicrographs, equipment diagrams, etc.

Where each figure is first referred to, type "Fig. — near here."

Computer-generated figures should be avoided if possible, as they usually reproduce poorly. Dot-matrix printers cannot produce sufficiently dark, solid lines to ensure legibility. Figures drafted in black india ink are always preferable. If sheets of printed characters are used, be sure they adhere completely.

Draft rather than type axis labels for graphs.

Color plates are very expensive to produce and should only be used where the color being presented is essential to the understanding of the text. Extra costs for the reproduction of color plates are usually charged to the author. Submit only the most outstanding photographs for color reproduction. We prefer to use color photographs, but will accept drawings, color negatives, slides, or film positives.

Mathematical Expressions, Equations, and Formulae

Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulae. In the various expressions, place each component in its correct position.

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital *O* and the numeral *zero*. Make other explanatory notes similarly.

Appendix

Abbreviations

Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

Becquerel	Bq
calorie	cal
centimetre	cm
centimetre, square	cm^2
centimetre, cubic	cm^3
centimetre per gram per second	$cm \cdot g^{-1} \cdot s^{-1}$
coulomb	C
day	d
decimetre	dm
degree Celsius	°C
degrees of freedom	df
gram	g
hectare	ha
hertz	Hz
hour	h
joule	J
kilometre	km
litre	L
lumen	lm
lux	lx
metre	m
metre, square	m^2
metre, cubic	m^3
micrometre	μm
milligram	mg
millilitre	mL
millimetre	mm
millimetre, square	mm^2
minute	min
molar mass	g/mol
mole	mol
month	mo
Pascal	Pa
second	s
standard deviation	SD
standard error	SE
tonne	t
volt	V
volume	vol
watt	W
week	wk
year	yr

Dates

Dates may be written in the sequence day–month–year without internal punctuation (On 9 October 1983 the ...), or the alternative sequence month–day–year may be employed with the year set off by commas before and after it (On October 9, 1983, the ...).

Reference Citations in Text

Name-and-year system

The *Journal* uses the name-and-year system of citation; that is, the surname of the author(s) and the year of publication are inserted in the text at an appropriate point: "Brown (1983) compared ..." or "... were compared (Brown 1983)." If the reference has more than two authors, include only the surname of the first author followed by "et al." (not italicized): "Brown et al. (1983) compared ..." or "... were compared (Brown et al. 1983)."

Personal communications

Personal communications are not listed in the reference list. Using parentheses in the text, state the name and mailing address of the communicator followed by "pers. comm."

Unpublished data

If the unpublished book or article has been accepted for publication, list it in the reference list section followed by the notation "(In press)." Only those manuscripts that are in galley or page proof or for which there is an acceptance letter can be considered in press. If the article is submitted but not yet accepted, state the name and address of the author of the unpublished material followed by the notation "unpubl. data" in the text and do not include it in the reference list.

Reference Lists

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *Serial Sources for the BIOSIS Data Base*) for references.

Journal article

PETERMAN, R. M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. 39: 1444–1452.

Entire issue of journal

GORDON, D. C. JR., AND A. S. HOURSTON [ED.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40 (Suppl. 1): 1–365.

Book in a series

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Book not in a series

LEBLOND, P. H., AND L. A. MYSAK. 1978. Waves in the ocean. Elsevier, New York, NY. 602 p.

Part of book

HEALEY, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia, p. 203–229. *In* W. J. Neil and D. C.

Himsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, OR.

Corporate author

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, DC. 1193 p.

Theses

Kutty, M. N. 1966. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, Univ. Toronto, Toronto, Ont. 102 p. Natl. Libr. Can., Can. Theses Microfilm No. 646.

Reports

Smith, J. E. 1981. Catch and effort statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1032: 90 p.

Translation

Koike, A., and M. Ogura. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64: 1–11. (Transl. from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983)

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h," "min," and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Word List

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the *Journal*'s house style for these commonly used terms:

age-class (n.)
age-group (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
short term (n.)
short-term (adj.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t-test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

Guide des auteurs

Introduction

Les manuscrits comportant une information nouvelle dans le domaine des sciences halieutiques et aquatiques sont les bienvenus. Ils peuvent se rapporter aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influencent les systèmes de production aquatiques, et couvrir de nombreuses disciplines, y compris biologie et écologie des organismes marins et dualçaquicoles, physiologie, toxicologie, génétique, limnologie, océanographie, économique, maladies et gestion.

Les critères de sélection des manuscrits dépendent de l'étendue et de l'importance des connaissances ou idées nouvelles qu'ils contiennent. On donnera la préférence à ceux dont les résultats expérimentaux font ressortir les mécanismes sous-jacents aux phénomènes observés plutôt qu'une simple description ou énoncé de fait. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles en faisant plus que corroborer des faits.

Les manuscrits soumis devraient être aussi complets que possible; des fragments de recherche sont généralement inacceptables. S'il était impossible de produire un seul article, on devra soumettre ensemble des articles étroitement liés entre eux, avec références croisées. L'article ne doit pas avoir été soumis ou accepté pour publication ailleurs.

Le *Journal* considère les types de contributions suivants:

Articles: Études d'une portée générale, constituant des contributions inédites à la science.

Notes: Communications brèves signalant une connaissance nouvelle et significative découlant de problèmes étroitement limités et facilement définis, ou d'importantes découvertes qui méritent d'être publiées avant que des études plus vastes soient terminées. Les notes ne doivent pas dépasser 3 pages imprimées (9 pages de manuscrit).

Critiques: Appréciations critiques détaillées de vastes champs de recherche, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais portant sur une opinion ou une hypothèse relative aux sciences aquatiques qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Commentaires: Opinions sur des sujets récemment exposés dans le *Journal*, et, de préférence, ne dépassant pas 500 mots.

Soumission des manuscrits

Les manuscrits doivent être soumis au rédacteur en triplicata, et accompagné d'une lettre mentionnant: (1) les principaux points et l'importance du travail, (2) l'acceptation des frais de publication obligatoires, (3) des suggestions quant aux arbitres éventuels et (4) une mention d'autres manuscrits contenant une information identique ou qui se rapproche de celle contenue dans le manuscrit soumis. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les simili) jusqu'à ce qu'on les lui demande.

Un manuscrit est normalement soumis à deux arbitres pour évaluation, avant l'évaluation finale par un rédacteur. Cependant, les manuscrits qui ne répondent pas à la politique éditoriale ou à la portée du *Journal* sont retournés à l'auteur sans avoir été soumis à l'arbitrage.

Dispositions générales

Le *Council of Biology Editors Style Manual* (5e éd., CBE, 9650 Rockville Pike, Bethesda, MD 20814) sert de guide quant à la forme de la présentation. Le *Webster's Third International Dictionary* ou l'*Oxford English Dictionary*, et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. L'uniformité de cette dernière est la responsabilité des auteurs. Les titres de périodiques sont abrégés suivant les *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103). Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (4e éd. 1980), Spec. Publ. No. 12, American Fisheries Society. Toutes les mesures doivent être conformes au système métrique et, dans la plupart des cas, être exprimées en unités SI (sauf exceptions mentionnées dans un éditorial du *Journal*, vol. 41, n° 1), et se conformer qu *Guide de familiarisation au système métrique* CAN3-Z234.1-79 (l'Association canadienne de normalisation, 178, boulevard Rexdale, Rexdale (Ont.) M9W 1R3).

On devra éviter les titres en séries. Un résumé doit doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé.

L'auteur doit revoir les épreuves qu'on lui remet et en corriger les erreurs typographiques. *Il doit éviter de modifier le contenu du texte.*

Cinquante tirés à part sont fournis gratuitement. Des tirés à part supplémentaires peuvent être achetés au moment de la publication (un bon de commande à cet effet accompagne les épreuves).

Préparation des manuscrits

Directives générales

La marche des manuscrits à travers les diverses étapes de l'arbitrage et de la révision sera grandement facilitée si les articles sont préparés dans le style et le format du *Journal*. En cas de doute sur des points particuliers, veuillez consulter une livraison récente du *Journal*. On trouvera ci-dessous des directives générales.

Dactylographiez le manuscrit sur papier blanc, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces), sur un côté de la page. Si possible, employez un papier avec lignes numérotées en marge. Laissez toujours une marge d'au moins 2,5 cm.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Tout le manuscrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique.

En aucun endroit du manuscrit n'écrivez entièrement en majuscules. Dans les tableaux et les en-têtes, n'employez la majuscule que pour la première lettre de chaque mot.

Pour les références citées dans le texte, utilisez le système nom et année.

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et rédacteurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Il a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le même texte? Est-ce que certaines données devraient être présentées séparément dans dans un rapport manuscrit ou dans un dépôt de données?

Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la recherche? Dans des énoncés de probabilité, seuls les tests statistiques sont-ils cités, et les tableaux statistiques inutiles sont-ils exclus?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il représentatif du contenu du rapport? Le *résumé* donne-t-il l'essentiel des connaissances nouvelles? L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème? La section *matériel et méthodes* contient-elle le minimum de détail qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données? Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Sont énumérés ci-dessous les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

1) Insérez la bande bibliographique avant le résumé (auteurs, date, titre, Can. J. Fish. Aquat. Sci.)

2) Limitez le résumé à un paragraphe d'environ 175 mots.

3) Dactylographiez à double interligne tous les éléments du manuscrit, y compris les références et les légendes des tableaux et des figures.

4) Évitez partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.

5) Ne soulignez que les noms latins d'organismes et certaines notations statistiques et mathématiques, qui devront être imprimées en italique.

6) Dans les figures, les tableaux et le texte, exprimez les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placez un zéro avant le point ou la virgule décimale.

7) Évitez les formes ambiguës, telles que $gC/m^2/d$; utilisez plutôt $gC\cdot m^{-2}\cdot d^{-1}$.

8) Identifiez le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire d'en donner la référence.

9) Dans le texte, généralisez à partir des tableaux et des figures; évitez une répétition de tous les détails. Assurez-vous que chaque tableau et figure sont indépendants et que, dans le texte, on y réfère dans l'ordre numérique. Les legendes doivent indiquer le but du tableau ou de la figure.

10) Préparez la section remerciements au stade du manuscrit et non quand vous parviennent les épreuves.

11) En référant à des communications personnelles, donnez les initiales et l'adresse postale de la personne en cause.

12) Éliminez toutes références inutiles qui ne s'appliquent pas directement au problème.

13) Vérifiez soigneusement les références contre les citations dans le texte et vice versa, afin de vous assurer qu'il y a correspondance. Dans le cas de matériel difficilement accessible, indiquez l'endroit où le trouver, p. ex., disponible auprès du Département de l'économique, Université Simon Fraser, Burnaby (C.-B.) V5A 1S6.

14) Éliminez les virgules entre le nom et la date dans les citations telles que (Smith 1900) et soulignez *et al.*

15) Dans les en-têtes de tableaux et les axes des figures, remplacez 10^n par des préfixes SI appropriés ou utilisez des mots en clair (p. ex., milliers).

16) Aux fins de révision, des photocopies de figures, sauf simili, sont appropriées. Sur demande, lorsqu'il s'agira de publier, l'article, envoyez des photographies des figures, ou encore les originaux, s'ils ne dépassent pas 21,5 × 28 cm. Utilisez autant que possible un lettrage uniforme.

Parties du manuscrit

Organisation

Organisez le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dressez une liste provisoire des sous-titres ou en-têtes, avec le moins d'ordres possibles. Retouchez-les jusqu'à ce qu'ils semblent assurer, pour le lecteur, une marche logique; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'évaluer les résultats, si vous décrivez méthodes, résultats et discussion dans des sections séparées.

Organisez les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. Assurez-vous que ces derniers sont aussi clairs que possible sans référence au texte.

Commencez les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particuliers. Si vous donnez d'abord une conclusion que vous appuyez ensuite, non seulement votre travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction de manuscrits, le défaut le plus commun est le manque à donner, au début, les généralités les plus dignes de mention.

Voyez à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger un paragraphe, composez la première phrase de chaque paragraphe et disposez ces phrases dans l'ordre approprié.

Titre

Limitez le titre à ce que le travail veut démontrer. C'est la clé de l'article, et il devrait montrer clairement et de façon concise ce qui est contenu dans le travail lui-même. Le titre a deux fonctions: (1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et (2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance possible de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, lorsque approprié, la méthode d'approche technique (p. ex., rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à ... » ou « Recherches sur ...» De bons titres facilitent beaucoup l'utilisation des publications par les scientifiques et les bibliothécaires, et aident les préposés à l'indexation qui doivent préparer les titres pour les index de mots clés.

Résumé

Le résumé doit refléter succintement le contenu et les points principaux de l'article en 175 mots environ. Comme le titre, le résumé permet aux lecteurs de déterminer le contenu de l'article et décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquez au début du résumé la principale conclusion de l'étude et appuyez-la par des découvertes pertinentes. Ne donnez que les détails des méthodes nécessaires à la compréhension de ce qui a été fait et insérez-les dans l'énoncé des découvertes. Évitez l'emploi de phrases telles que « ... on y analyse » ou «... a été trouvé »; soyez spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services analytiques et d'indexation, et que c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir, il est important que le résumé reflète précisément le contenu du travail.

Introduction

Limitez l'introduction à la portée, au but et à la raison de l'étude. Dans votre analyse des travaux publiés et autre information de base, ne donnez que ce qui est nécessaire à la définition du problème et à la perspective du travail. Commencez avec le but ou la portée du travail, définissez ensuite le problème et ajoutez ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375–500 mots.

Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limitez les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si vous présentez, autant que possible, toute l'information dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référez à ces publications et ne décrivez en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme, par exemple: « Afin de déterminer ... nous ... » Si la section est longue, songez à utiliser des sous-titres correspondant à ceux que vous utilisez dans la section résultats.

Résultats

Limitez les résultats aux réponses apportées aux questions en rapport avec le but de l'étude; que ces réponses soient aussi complètes que possibles, tout en étant concises. Exprimez ce que vous avez trouvé, autant que possible dans les mêmes termes que ceux dans lesquels les observations ou les mesures ont été faites, évitant ainsi de confondre fait et spéculation. En dégageant les généralités des tableaux et des figures, référez-y et évitez de répéter dans le texte ce que les légendes devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans la série des rapports ou dans un dépôt de données reconnu, et on y référera dans le texte.

Discussion

Limitez la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synthèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, notez-les et faites ressortir la manière dont vos résultats corroborent ou contredisent les travaux déjà publiés. Limitez la spéculation à ce que vous pouvez appuyer sur des preuves raisonnables. Terminez cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et au point, elle peut être combinée avec les résultats en une seule et même section.

Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements à ceux qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou ammélioré la qualité de la présentation. Évitez de mentionner ceux dont la contribution n'a été que cléricale.

Références

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux et communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (indiquez les adresses postales). Si l'on doit citer des rapports d'experts-conseils ou autres documents dont la distribution est limitée, on devra préciser l'encroit où l'on peut se les procurer. Les références mentionnées dans le texte doivent être soigneusement vérifiées contre celles contenues dans la liste de références et vice versa, afin de s'assurer qu'il y a correspondance. Presque tous les manuscrits soumis au *Journal* contiennent des erreurs sous ce rapport.

Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible.

Agencez les tableaux de façon qu'ils s'adaptent soit à une colonne ou à une page du *Journal*.

Dactylographiez chaque tableau sur page séparée et numérotez-les en chiffres arabes.

Tracez des lignes horizontales au-dessous des en-têtes et des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplémentaires.

Chaque tableau doit avoir une légende instructive, complète et indépendante.

Les renvois des tableaux doivent être indiqués par des petites lettres suscrites dactylographiées au bas du tableau.

Placez les tableaux après la liste des références.

Quand on réfère à un tableau pour la première fois, on indique dans la marge du manuscrit « Tableau — près d'ici ».

Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le texte lui-même. Ils ont rarement besoin de lignes horizontales.

Figures

Fournissez des photographies ou les dessins originaux (pourvu qu'ils ne dépassent pas 21,5 × 28 cm) de chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas sur l'illustration elle-même. Transmettez deux photocopies des dessins au trait et deux séries de photos qui serviront au moment de la révision.

Les dessins devront être préparés à échelles équivalant à 1, 2 ou 3 largeurs de colonne du *Journal*. Assurez-vous que toutes les lettres, chiffres et symboles sont lisibles, clairs et d'au moins 1,5 mm de hauteur une fois réduits. Les figures ne devraient pas être montées, brochées ou fixées à l'aide de trombones. Autant que possible, elles devraient être groupées et préparées avec le même type de lettrage.

Dactylographiez les légendes, dans l'ordre, sur feuilles séparées. Dans le cas de cartes, photomicrographies, diagrammes d'instruments, etc., ajoutez une échelle.

À l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge « Fig. — près d'ici ».

On devra autant que possible éviter les illustrations préparées par ordinateur, car elles ne se reproduisent pas très bien. Les imprimantes par points ne peuvent produire de lignes solides suffisamment foncées pour être lisibles. On obtiendra toujours de meilleurs résultats en utilisant de l'encre de Chine noire. Si vous utilisez des feuilles de caractères imprimés, assurez-vous de leur complète adhérence.

Dessinez plutôt que dactylographiez les inscriptions relatives aux axes.

La production de planches en couleurs est très dispendieuse et on ne devrait les utiliser que quand les couleurs sont essentielles à la compréhension du texte. Les coûts supplémentaires de reproductions de planches en couleurs sont ordinairement imputés à l'auteur. Pour reproductions en couleurs, ne soumettez que des photos d'excellente qualité. Nous préférons utiliser des photographies en couleur, mais acceptons dessins, négatifs, diapositives ou positifs de films en couleurs.

Expressions, équations et formules mathématiques

Laissez trois espaces au-dessus et au-dessous des lignes contenant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre.

Indiquez clairement tous les symboles. Épelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Abréviations

N'abrégez les termes désignant les unités de poids et mesures dans le texte que lorsqu'ils sont précédés de nombre.

an	an
année	a
Becquerel	Bq
calorie	cal
centimètre	cm
centimètre carré	cm^2
centimètre cube	cm^3
centimètre par gramme par seconde	cm·g^{-1}·s^{-1}
coulomb	C
décimètre	dm
degré Celsius	°C
degrés de liberté	dl
écart type	EcT
électrovolt	eV
erreur type	ErT
farad	F
gram	g
hectare	ha
hertz	Hz
heure	h
joule	J
jour	d
kilomètre	km
litre	L
lumen	lm
lux	lx
mètre	m
mètre carré	m^2
mètre cube	m^3
micromètre	µm
milligramme	mg
millilitre	mL
millimètre	mm
millimètre carré	mm^2
minute	min
mois	mo
masse molaire	g/mol
mole	mol
Pascal	Pa
seconde	s
semaine	sem
tonne	t
volt	V
volume	vol
watt	W

Dates

On écrira les dates dans l'ordre jour–mois–année, soit le 9 octobre 1983, … sans virgule entre le mois et l'année.

Citations de références dans le texte

Système de nom et année

Le *Journal* utilise le système de nom et année, ci.-à-d. le nom de ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié: « Brown (1983) compare ...» ou «... on a comparé (Brown 1983) ». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de « *et al.* »: « Brown *et al.* (1983) comparent ...» ou «... on a comparé (Brown *et al.* 1983) ».

Communications personnelles

Les communications personnelles ne sont pas incluses dans la liste des références. Utilisez plutôt des paranthèses dans le texte, entre lesquelles vous indiquerez le nom et l'adresse postale de la personne en question, suivis de « comm. pers. »

Données inédites

Si le livre ou l'article inédits ont été acceptés pour publication, insérez-les dans la liste des références, avec la mention « (Sous presse) ». On ne peut considérer comme étant sous presse que les manuscrits au stade d'épreuves ou ceux couverts par lettre d'acceptation. Si l'article a été soumis mais n'a pas encore été accepté, ne l'incluez pas dans la liste de références, mais indiquez le nom et l'adresse de l'auteur du matériel inédit, dans le texte lui-même, avec la mention « données inédites ».

Liste de références

La liste qui suit donne des exemples de ponctuation, de style et d'abréviations utilisés dans les références bibliographiques (d'après les *Serial Sources for the BIOSIS Data Base*).

Article du journal

Archambault, D. et E. Bourget. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieu subarctique. Can. J. Fish. Aquat. Sci. 40: 1278–1292.

Numéro complet du journal

Gordon D. C., Jr. et A. S. Hourston [éd.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40 (Suppl. 1): 1–365.

Livre dans une série

Hilton, J. W. et S. J. Slinger. 1981. nutrition et alimentation de la truite arc-en-ciel. Publ. spéc. can. sci. halieut. aquat. 55: 17 p.

Livre non dans une série

Forrester, W. D. 1983. Manuel canadien des marées. Ministère des Pêches et des Océans, Service hydrographique du Canada, Ottawa (Ont.). 148 p.

Partie d'un livre

Aubert, M., J. Aubert, S. Daniel et N. Desirotte. 1972. Etat actuel de la pollution bactérienne au large des côtes françaises, p. 36–40. *Dans* M. Ruivo [éd.] La pollution des mers et les ressources biologiques. Fishing News (Books) Ltd., Londres.

Corporation-auteur

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14e éd. Washington, DC. 1193 p.

Thèse

Delisle, C. 1969. Ecologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la repartition en eau douce du Québec. Thèse doctorale, Univ. Ottawa, Ottawa (Ont.). 161 p.

Rapports

Dutil, J. D., M. Fortin et Y. Vigneault. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement de Québec. Rapp. manus. can. halieut. aquat 1653: 29 p.

Traduction

Koike, A. et M. Ogura. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64: 1–11. (Traduit du japonais par Can. Transl. Fish. Aquat. Sci. 4950, 1983)

Temps

On devra séparer les deux points (:) heure et minute, et minute et seconde. Les symboles « h », « min » et « s » ne sont pas utilisés car ils représentent heure, minute et seconde dans le sens de durée ou intervalle de temps. C'est ainsi que « 12 h 30 min » exprime un intervalle de temps de douze heures et trente minutes, alors que 12:30 se rapporte à l'heure du jour.

Liste de mots

Cette section, dans la version anglaise du Guide, contient une série de mots dont l'orthographe pose certains problèmes d'uniformité, comme, par exemple, « cold water » (n.), « cold-water » (adj.); « hard water » (n.), « hardwater » (adj.), etc. L'auteur préparant un texte en anglais est prié de consulter la version anglaise du Guide.

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